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Vol. 85, No. 1 January 1987

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The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. In this form, it is available by subscription from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402. It is also available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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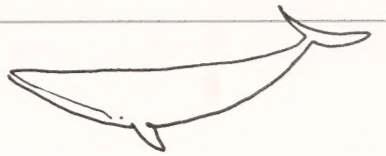

The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* and the *Marine Fisheries Review* for 1984 and 1985. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers were judged as the best in meeting this requirement:

Fishery Bulletin 1984, from the Systematics Laboratory, Washington, D.C. — "Morphology, systematics, and biology of the Spanish mackerels (*Scomberomorus*, Scombridae)" by Bruce B. Collette and Joseph L. Russo. [FB 82(4):545-692.]

Fishery Bulletin 1985, from the Southwest Fisheries Center Honolulu Laboratory, Honolulu, Hawaii — "Using objective criteria and multiple regression models for age determination in fishes," by George W. Boehlert. [FB 83(2):103-117.]

Marine Fisheries Review 1984, from the Southwest Fisheries Center Honolulu Laboratory, Honolulu, Hawaii — "Ground fisheries and research in the vicinity of seamounts in the North Pacific Ocean," by Richard N. Uchida and Darryl T. Tagami. [MFR 46(2):1-17.]

For special recognition — Marine Fisheries Review Vol. 46, No. 4, pages 1-64:

"The status of endangered whales: an overview," by Howard W. Braham. (Pages 2-6.)

"The gray whale, *Eschrichtius robustus*," by Dale W. Rice, Allen A. Wolman, and Howard W. Braham. (Pages 7-14.)

"The blue whale, *Balaenoptera musculus*," by Sally A. Mizroch, Dale W. Rice, and Jeffrey M. Breiwick. (Pages 15-19.)

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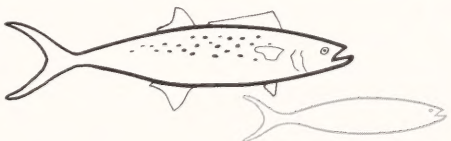

PATTERNS OF LARVAL DRIFT IN SOUTHERN CALIFORNIA MARINE SHORE FISHES INFERRED FROM ALLOZYME DATA

ROBIN S. WAPLES[1] AND RICHARD H. ROSENBLATT[2]

ABSTRACT

A multispecies analysis of allozyme data for 10 marine shore fishes was undertaken to identify patterns of genetic differentiation resulting from larval drift. Previous studies suggest that allele frequencies in these fishes are sensitive primarily to the effects of migration, rather than to natural selection or historical factors. The following patterns recur in most species: 1) Two northern populations (La Jolla, California, and the California Channel Islands) share a relatively high genetic affinity with all other populations, while the two southern populations (Isla de Guadalupe and Punta Eugenia, Baja California, Mexico) are relatively divergent; 2) the two southern populations apparently exchange genes much more frequently with northern populations than with each other; 3) anomalous results for the ocean whitefish, *Caulolatilus princeps*, can be understood on the basis of known patterns of larval distribution in this species. The consistency of these large-scale patterns among species with markedly different life history features and dispersal capabilities suggests that the results obtained here may provide insight into the population structure of other species (invertebrates as well as fish) with pelagic larvae.

Two characteristics of shallow-water marine organisms make the analysis of their population structure interesting and challenging. First, adults of these species are restricted to relatively shallow, inshore waters, so adult populations can be isolated from other populations by expanses of deep water or areas of otherwise unsuitable habitat. On the other hand, many marine species have a pelagic larval stage lasting several weeks or months and thus at least the potential for long-distance transport by ocean currents. Indeed, such long-distance dispersal events are generally invoked to explain the presence of shallow-water marine organisms on oceanic islands isolated by up to several thousand kilometers from possible sources of propagules.

However, very little is actually known concerning the complex process of larval drift, and several questions remain largely unanswered. For example, by what pathways do larvae traverse oceanic barriers separating different populations? Furthermore, do recruits arrive at remote areas on a more-or-less continuous basis, or is long-distance dispersal the result of rare or unique "sweepstakes" events? The answers to these questions are relevant not only to evolutionary biologists seeking to understand the processes of differentiation and speciation, but also to those who, in order to formulate management policies for marine fishery resources, must determine the degree to which geographic stocks correspond to independent reproductive units.

Several approaches have been used to address the problem of pelagic dispersal. In some cases, sufficient data regarding oceanic currents are available to construct models capable of predicting patterns of larval distribution if time and place of spawning are known. However, as such models are generally based on long-term mean current patterns, they may be misleading if successful dispersal is actually due to anomalous conditions that occur infrequently. Furthermore, few data are available regarding the inshore currents intimately involved in the initial dispersion (or retention) of larvae spawned in shallow water. Marked drifters (e.g., Schwartzlose 1963; Tegner and Butler 1985) can provide biologically relevant data regarding current patterns, but such studies rely on retrieval by the human population at large and thus provide little information about dispersal to remote (and typically poorly inhabited) localities. Tagging studies, although very resource intensive, can provide valuable, direct information regarding oceanic migrations but are not well-suited to the study of larval drift.

For the above reasons, indirect methods must often be used to estimate the incidence of gene flow in marine organisms. The electrophoretic analysis of protein polymorphisms is one such approach that has seen extensive use in both terrestrial and aquatic

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systems. Electrophoretically detectable allele frequencies can be used to estimate levels of migration if it can be assumed that these frequencies reflect a balance between the opposing forces of migration (gene flow) and random divergence of allele frequencies (genetic drift). The main difficulty with this approach is that other forces, notably natural selection and historical contact, can influence allele frequencies, and the relative importance of these forces in natural populations has proved extremely difficult to evaluate directly.

The present study differs from most previous ones in an important way: rather than concentrate on one or two species, we sampled 10 marine shore fishes from the same suite of island and mainland localities in southern California and Baja California, Mexico. Substantial differences between species in fecundity, length of larval life, and other life history features allowed us to test the hypothesis that species with low dispersal capability should show greater genetic differences between populations than do species that are better dispersers. As discussed by Waples (in press), the statistically significant negative correlation between dispersal capability and levels of genetic differentiation in these shore fishes is consistent with expectations based on an equilibrium model involving gene flow and genetic drift. Scenarios invoking natural selection and/or historical (nonequilibrium) perturbations of migration patterns could be hypothesized to explain these results, but there is no a priori reason to expect the observed correlation to result from selection or historical factors. The test discussed by Waples (in press) does not exclude the possibility of selection at individual gene loci, but does suggest that such forces have not been strong enough to disturb the overall patterns of genetic differentiation due to gene flow that are of interest here.

In this paper we extend the analysis of these data to address two questions regarding larval dispersal that can only be understood by considering data for a number of species simultaneously: 1) Are there consistent patterns (across species) of genetic similarity among localities that suggest common avenues of larval transport? 2) If such patterns do exist, can results for those species that are exceptions to the pattern be understood in terms of different behavioral or life history features that might cause their larvae to be affected differently by the current regime? The question of the frequency of successful long distance dispersal in these shore fishes and some of the problems associated with estimating this frequency will be discussed in a later paper.

MATERIALS AND METHODS

Experimental Design

Collections were made at six sites in four major areas: La Jolla, CA; the California Channel Islands (San Nicolas Island and Santa Catalina Island); Isla de Guadalupe, Mexico; and near Punta Eugenia, Mexico (Cabo Thurloe and Islas de San Benito; see Figure 1). Two sites were used in the Channel Islands and near Punta Eugenia because not all species could be collected at a single locality. The area of study describes a quadrilateral roughly 600 km long and 100-300 km wide that encompasses almost the entire area south of Point Conception governed by the California Current System. Furthermore, few of the species studied occur north of Point Conception in any numbers, and central Baja California, Mexico, is at or near the southern distributional limit for most of these species as well. The study areas thus cover a major portion of the normal range for these species, and this sampling pattern should have been able to detect significant population subdivision if it exists.

The study sites were also chosen in such a way that the genetic affinities of populations in certain areas could be evaluated. Mainland populations are represented by samples taken at La Jolla. The California Channel Islands harbor large populations of many marine organisms, and it is important to assess the degree to which these populations are independent of those from the mainland. Guadalupe is a small, oceanic island of volcanic origin surrounded by deep (>3,000 m) water. It is remote enough (275 km west of the central Baja California coast) that genetic differentiation of shore fishes might be expected. Collections in the vicinity of Punta Eugenia were made to serve as controls for evaluating the extent of differentiation at Guadalupe and to estimate the relative importance of east-west larval drift in this area.

Well-developed oceanic currents serve as potential transport mechanisms for pelagic larvae in the study area. The California Current brings relatively cold, low salinity water from high latitudes toward the Equator; its principal characteristics have been known for some time (Reid et al. 1958; Hickey 1979). The California Current is most strongly developed north of Point Conception; further south, nearshore flow becomes somewhat variable because of the eastward jut of the coastline and the complicating effects of the Channel Islands (Fig. 1). Between about lat. 30° and 33°N, the current shifts toward the east, and a portion of the water is deflected

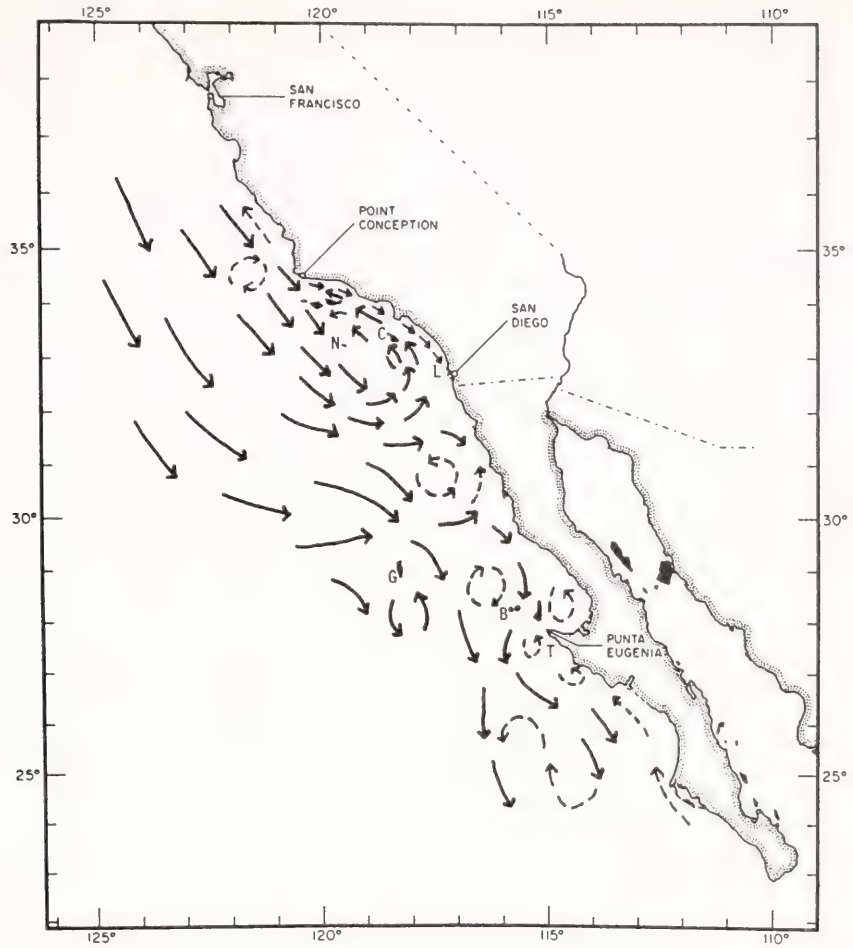

FIGURE 1.—Schematic representation of mean flow patterns in the study area, based on data from Wyllie (1966) and Hickey (1979) and modified from Cowen (1985). Consistent flow directions are shown with solid arrows; dashed arrows indicate more variable features. Study sites are also indicated: La Jolla (L); San Nicolas (N) and Catalina (C), California Channel Islands; Isla de Guadalupe (G); Islas de San Benito (B); Cabo Thurloe (T).

northward along the Southern California Bight, forming the Southern California Eddy (Schwartzlose 1963). This eddy can be found throughout the year except during periods of peak southward flow (generally January to May).

The 10 shore fish species used in the analysis (Table 1) were generally those that could be collected in adequate numbers during brief visits to remote localities. However, attempts were made to include species with widely varying life history strategies and, hence, different dispersal capabilities. The life history and larval capture data summarized in Table 1 were taken from personal observations, unpublished data from the California Cooperative Fisheries Investigations (CalCOFI) and the Ichthyoplankton Coastal and Harbor Studies (ICHS), and from the literature; see Waples (1986) for discussion and references. Sample sizes of about $N = 50$ individuals per species were collected at each of the four areas [ranges of mean sample sizes: for species, $\bar{N} = 36$ (blacksmith) to $\bar{N} = 63$ (sheephead); for localities, $\bar{N} = 46$ (Punta Eugenia) to $\bar{N} = 55$ (Guadalupe)].

Electrophoresis and Data Analysis

Whole fish or tissue samples were frozen in the field, transported to Scripps Institution of Oceanography, and stored at −25°C to −35°C. Procedures of horizontal starch gel electrophoresis and

TABLE 1.—Summary of life history information for the 10 shore fish species used in the analysis.

Family/species	Common name	Batch fecundity	Length of larval life	Larval catches	Dispersal capability
Embiotocidae					
Embiotoca jacksoni	black perch	10	none (viviparous)	—	nil
Cottidae					
Clinocottus analis	wooly sculpin	10^2-10^3	few weeks?	only near rocky shores	low
Clinidae					
Alloclinus holderi	island kelpfish	10^3	brief?	inshore?	limited
Gobiidae					
Lythrypnus dalli	bluebanded goby	10^2-10^3	two or more months	inshore	moderate
Malacanthidae					
Caulolatilus princeps	ocean whitefish	10^5	few months?	inshore/offshore	high
Pomacentridae					
Chromis punctipinnis	blacksmith	10^5	few months?	inshore/offshore	high
Kyphosidae					
Girella nigricans	opaleye	10^5	few months?	mostly inshore	high
Serranidae					
Paralabrax clathratus	kelp bass	10^5	few months?	mostly inshore	high
Labridae					
Semicossyphus pulcher	sheephead	10^5	2-4 months	inshore/offshore	high
Kyphosidae					
Medialuna californiensis	halfmoon	10^5	few months	offshore	very high

histochemical staining have been described elsewhere (Waples 1986). The 26 enzymes and proteins surveyed were acid phosphatase, aconitate hydratase, adenosine deaminase, adenylate kinase, alchohol dehydrogenase, aspartate aminotransferase, creatine kinase, esterase (α-naphthyl acetate), fumarate hydratase, glucose-6-phosphate dehydrogenase, glucosephosphate isomerase, glutamate dehydrogenase, glyceraldehyde-phosphate dehydrogenase, glycerol-3-phosphate dehydrogenase, L-iditol dehydrogenase, isocitrate dehydrogenase, lactate dehydrogenase, malate dehydrogenase, mannosephosphate isomerase, phosphoglucomutase, phosphogluconate dehydrogenase, peptidase (leucyltyrosine; leucylglycyl-glycine), superoxide dismutase, umbelliferyl esterase, xanthine dehydrogenase, and general muscle proteins. Presumptive gene loci for which any variant alleles were detected were surveyed in all individuals. Loci for which only a single allele had been identified after sampling at least 20 individuals in each population were considered to be monomorphic and were not surveyed further in that species.

Wright's F_{ST} was computed for each polymorphic locus in each species by the method of Weir and Cockerham (1984). F_{ST} values ($0 \leqslant F_{ST} \leqslant 1$) indicate the proportion of total variance in allele frequencies attributable to differences between (as opposed to within) populations. Workman and Niswander's (1970) test was used to identify F_{ST} values significantly larger than zero. Data for all presumptive gene loci resolved in each species were combined in an index of overall genetic differentiation (Nei's [1972] genetic distance (D)), which provides a direct means of comparing levels of genetic divergence between pairs of populations. D is the negative natural logarithm of genetic similarity (I), which is essentially the proportion of genes shared by two populations.

To determine whether similar patterns of population structure occur in several species, D values for each pair of localities (or the mean D values for each locality) were ranked within each species. The resulting matrix of rankings was evaluated for recurring patterns (departure from randomness) by Friedman's method for randomized blocks (Sokal and Rohlf 1981), which computes a statistic that is a chi-square variate with $b - 1$ degrees of freedom:

$$\chi^2_{(b-1)} = [(12/(ab[b+1])) \sum^{b} (\sum^{a} R_{ij})^2] - 3a(b+1) \quad (1)$$

where a = number of rows (species, in this case), b = number of columns (localities, or pairs of localities), and R_{ij} is the ranking of the i^{th} locality (or pair of localities) for the j^{th} species.

To identify species that exhibit anomalous patterns of genetic differentiation, a jackknife procedure was used, the rankings of localities (or pairs of localities) for each species being compared with the overall ranking computed for all the other species combined. Spearman's rank-order correlation coefficient (r_s) was used to determine the

strength of the agreement (or disagreement) between these two sets of rankings:

$$r_s = 1 - (6 \sum d_i^2/[n(n^2 - 1)]) \quad (2)$$

where n is the number of items ranked (in this case, 4 localities or 6 pairs of localities) and d_i is the difference in rankings of the i^{th} locality (or pair of localities).

RESULTS

The electrophoretic analysis provided information regarding variation at 32-42 presumptive gene loci in the 10 species. The genetic interpretation of banding patterns was guided by comparisons of observed and expected number of bands exhibited by presumed heterozygotes, by tissue specificity of isozyme expression, and by quality and consistency of resolution. A detailed discussion of results for each enzyme can be found in Waples (1986). Except for *Semicossyphus pulcher* (discussed below), no overall departures of heterozygote frequencies from those expected under conditions of Hardy-Weinberg equilibrium were found (Waples 1986, in press).

Table 2 summarizes the allozyme data. Average heterozygosities for the 10 species (mean $H = 0.031$; range = 0.009-0.087) are somewhat lower than the mean value of 0.055 reported for over 100 marine fishes by Smith and Fujio (1982), but at least 5 loci (*Embiotoca jacksoni*) and as many as 19 loci (*Lythrypnus dalli*) were found to be polymorphic in each species. Space does not permit reporting here the allele frequencies for all of these variable loci; these data appear in Waples (1986), or can be obtained from the first author.

Interpopulational genetic distance values (Table 2) were generally fairly small: for half of the species (*Alloclinus holderi*, *Chromis punctipinnis*, *Girella nigricans*, *Medialuna californiensis*, *Paralabrax clathratus*) all possible pairwise comparisons of populations yielded D values <0.001. Even the largest observed D value (0.029 for the Guadalupe-Punta Eugenia comparison in *E. jacksoni*) is well within the range of values typically found between conspecific populations of fish species (Shaklee et al. 1982; Thorpe 1983). Nevertheless, it is apparent that populations of most of these shore fishes do not behave as a single panmictic unit. For 8 of the 10 species, significantly nonzero single-locus F_{ST} values indicate heterogeneity of allele frequencies among populations (Table 2; see also Waples 1986). Furthermore, the statistically significant tendency for species that are better dispersers to have lower mean D values (Waples in press) suggests that the relatively small D values reported here for most species contain valid information relating to population structure.

Our interest here is primarily to identify recurring patterns (across species) of genetic similarity between areas. One way to approach this topic is to compute, for each species, a mean of all the pairwise D values involving each locality. In Table 3 these mean D values have been ranked within each species, thus providing an indication of which populations are most similar (or dissimilar) genetically to the other populations as a whole. Two species (*A. holderi*, *L. dalli*) that could be collected from only three of the four areas have been deleted from this analysis.

The two southern populations, Guadalupe and Punta Eugenia (total of rankings for each = 15), are consistently more divergent than are La Jolla (24.5) and San Nicolas (25.5). Substitution of these totals and values for a (8 species) and b (4 localities) into Equation (1) yields a χ^2 value of 7.54 with 3 df. This

TABLE 2.—Summary of electrophoretic results. Number of loci surveyed (T), number polymorphic (P), and number with significantly nonzero F_{ST} values (F) are indicated. H = average heterozygosity; L = La Jolla; C = Channel Islands; E = Punta Eugenia; G = Isla de Guadalupe.

Species	Number of loci				Genetic distance (× 10^2)					
	T	P	F	H	L-C	L-G	L-E	C-G	C-E	G-E
A. holderi	32	10	1	0.009	—	—	—	0.063	0.042	0.023
Ca. princeps	35	14	1	0.049	0.183	0.146	0.205	0.062	0.144	0.050
Ch. punctipinnis	40	10	1	0.009	0.007	0.021	[1]0.009	0.023	[1]0.012	[1]0.027
Cl. analis	36	17	10	0.046	0.158	0.293	0.237	0.269	0.158	0.362
E. jacksoni	40	5	4	0.015	0.665	0.457	1.55	1.45	0.338	2.87
G. nigricans	42	17	1	0.025	0.043	0.022	0.021	0.046	0.073	0.052
L. dalli	35	19	3	0.087	0.094	0.218	—	0.171	—	—
M. californiensis	38	18	—	0.025	0.022	0.019	0.024	0.018	0.037	0.054
P. clathratus	41	12	—	0.012	0.011	0.020	0.015	0.007	0.028	0.032
S. pulcher	38	14	3	0.033	0.009	0.178	[1]0.098	0.155	[1]0.070	[1]0.083

[1]Mean of comparisons involving Cabo Thurloe and Islas de San Benitos.

TABLE 3.—Chi-square test of homogeneity of ranking of areas by decreasing mean *D* values and correlation of ranking of areas in each species with overall ranking of all other species. Statistics computed for 8 species collected at all four areas and for the remaining 7 species after data for *Ca. princeps* were omitted. L = La Jolla; C = Channel Islands; E = Punta Eugenia; G = Isla de Guadalupe.

	Rankings by area				Correlation (r_s) with other species	
Species	L	C	E	G	8 spp	7 spp
Ca. princeps	1	3	2	4	−0.80	—
Ch. punctipinnis	4	3	2	1	0.60	1.0
Cl. analis	3	4	2	1	0.75	0.80
E. jacksoni	3	4	2	1	0.75	0.80
G. nigricans	4	1	2	3	−0.23	0.20
M. californiensis	4	3	1	2	0.60	0.80
P. clathratus	3.5	3.5	1	2	0.75	0.75
S. pulcher	2	4	3	1	0	0.40
	Totals				CSQ (3 df)	Signif. level
8 spp	24.5	25.5	15	15	7.54	NS
7 spp	23.5	22.5	13	11	10.59	$P < 0.05$

value is not quite significant ($0.1 > P > 0.05$; critical value 7.81). Although the pattern of differentiation over all eight species cannot be shown to depart significantly from randomness by this nonparametric test, it is instructive to continue the analysis to see whether anomalous results in one or two species may be obscuring an underlying pattern in the others. Aberrant species can be identified by measuring the correlation (r_s) of rankings for each species with the overall rankings for all other species combined. To do this, rankings for the localities were computed as each species in turn was deleted from the analysis. These rankings were then compared with those for the species deleted. The r_s values for this analysis clearly indicate a core group of five species (*Chromis punctipinnis, Clinocottus analis, E. jacksoni, M. californiensis, P. clathratus*), rankings for each of which are highly correlated with those of all other species (Table 3). At the other extreme, rankings of *Caulolatilus princeps* are essentially the opposite of those of the other species ($r_s = -0.80$). Thus *C. princeps* is the only species for which La Jolla was ranked the most divergent locality, as it is the only species for which Guadalupe is the locality with the highest overall genetic similarity to the other populations.

In order to evaluate the influence of *Caulolatilus princeps* on the overall analysis, Friedman's test was repeated after data for *C. princeps* had been deleted. The resulting chi-square value for seven species (10.59; 3 df) is significant at the 0.05 level. After omitting *C. princeps*, the correlation (r_s) for each species with all other species was again computed (Table 3). It is apparent that the remaining species form a more coherent group with *C. princeps* omitted, values for each species being positively correlated with those from all other species.

More detail regarding possible pathways of larval drift can be obtained by considering the relative degree of divergence of each pair of populations. *D* values for the six possible pairwise comparisons of the four study areas have been ranked within each species in Table 4. An analysis similar to the preceding indicates that the two northern populations (La Jolla and the Channel Islands) are consistently the most similar genetically, and the two southern populations (Punta Eugenia and Guadalupe) are the most divergent. There are no consistent differences in rankings of the four other comparisons, each of

TABLE 4.—Chi-square test of homogeneity of ranking of pairs of localities by decreasing mean *D* values and correlation of ranking in each species with overall ranking of all other species. Statistics computed for 8 species collected at all four localities and for the remaining 7 species after data for *Ca. princeps* were omitted. Abbreviations as in Table 3.

	Rankings of pairs of localities						Correlation (r_s) with other species	
Species	L-C	L-E	L-G	C-E	C-G	E-G	8 spp	7 spp
Ca. princeps	2	1	3	4	5	6	−0.77	—
Ch. punctipinnis	6	5	3	4	2	1	0.49	0.94
Cl. analis	5.5	4	2	5.5	3	1	0.46	0.93
E. jacksoni	4	2	5	6	3	1	0.14	0.26
G. nigricans	4	6	5	1	3	2	−0.16	0.31
M. californiensis	4	3	5	2	6	1	0.09	0.14
P. clathratus	5	4	3	2	6	1	0.43	0.54
S. pulcher	6	3	1	5	2	4	−0.03	0.54
	Totals						CSQ (5 df)	Signif. level
8 spp	36.5	28	27	29.5	30	17	7.09	NS
7 spp	34.5	27	24	25.5	25	11	11.84	$P < 0.05$

which involves one northern and one southern population. The same five species identified in the previous analysis (*Chromis punctipinnis, Clinocottus analis, P. clathratus, E. jacksoni, M. californiensis*) have the highest correlation with rankings of the other species, although only for the former three is $r_s > 0.40$. Again, results for *Caulolatilus princeps* ($r_s = -0.77$) are strongly negatively correlated with those of the other species. The chi-square value testing the equality of rankings for pairs of localities (7.09; 5 df) is not statistically significant (critical value = 11.07).

In light of the results obtained above, the analysis was repeated after deletion of *Caulolatilus princeps*. When this was done, the r_s values for each of the other species increased, to as high as 0.93 and 0.94 for *Clinocottus analis* and *Chromis punctipinnis*, respectively. The chi-square value (11.84) indicates that for the remaining species the rankings of pairs of localities are significantly heterogeneous. With data for *Caulolatilus princeps* omitted, it is even more apparent that the Guadalupe-Punta Eugenia comparison is the most divergent, and La Jolla-Channel Islands remains the most similar pair of localities (Table 4).

DISCUSSION

Two major points emerge from the analysis of patterns of genetic similarity between areas. First, large-scale patterns of larval dispersal for most species appear to be affected in a similar way by the local current regime. The recurrent patterns can be summarized as follows: 1) La Jolla and the Channel Islands are the two areas with the greatest (and Punta Eugenia and Guadalupe the two areas with the lowest) overall genetic affinity with other populations; 2) the two northern populations share similar allele frequencies, while the two southern populations have much stronger genetic affinities with the northern populations than with each other.

That the southern populations are relatively isolated genetically is not surprising, since they are at the periphery of the distributional range for most of the species. However, it was not expected that the Punta Eugenia populations would show nearly the same degree of genetic isolation as do those from Guadalupe, an oceanic island with a substantial endemic component in its marine flora and fauna (Briggs 1974). The nature of genetic differentiation of Guadalupe shore fishes is discussed more fully in Waples (1986). That many marine species with northern affinities are found along the coast of Baja California, Mexico only in localized upwelling areas (Dawson 1945; Hubbs 1960) may be responsible for the observed divergence of Punta Eugenia populations. These upwelling populations, isolated from other shore fish populations by areas with water temperatures up to 10°C warmer, may represent largely independent reproductive units. One aspect of the population structure that seems clear from the results of this study is that the southern populations studied exchange genes much more frequently with northern populations than with each other. Such a finding would be difficult to predict on the basis of known current patterns, which are quite variable and complex off the coast of Baja California (Fig. 1).

Because the southerly flowing California Current is the dominant hydrological feature in the study area, it is of interest to examine the possibility that the link between northern and southern populations is due primarily to one-way gene flow from the north. This possibility can be evaluated in terms of the presence or absence of rare alleles. If gene flow were unidirectional (north to south), one would expect most alleles present in the northern populations also to appear in samples from the south. Alleles originating in the southern populations, on the other hand, would have no tendency to spread to the north. For the 10 species combined, 50 alleles are found in one or more northern populations but are absent from all southern populations, while only 36 alleles are restricted to southern populations (Waples 1986).

These data thus do not provide evidence for gene flow only from the north, as such a model would predict more alleles restricted to southern populations. Furthermore, the average frequency of alleles restricted to the southern populations (0.0098) is slightly higher than the frequency of those restricted to the north (0.0092); this is the opposite of the result expected if unidirectional migration were "swamping" alleles restricted to the south. It is possible that the episodic northward advection of water from the south is an important source of genetic exchange among populations. Such movement is known to occur even in years not associated with El Niño events, and organisms with southern affinities that apparently have been transported into southern and central California are reported on a fairly regular basis (Hubbs and Schultz 1929; Hubbs 1948; Radovich 1961; Brinton 1981). The data for restricted alleles are consistent with the hypothesis that such processes may be important in the overall genetic structure of these shore fishes. Two factors, however, argue for caution regarding this conclusion: 1) the pattern of occurrence of restricted alleles is

quite variable among species, and four species have more alleles restricted to southern localities; 2) relatively few restricted alleles are found in these shore fishes, further increasing the already large sampling variation in the number and frequency of restricted alleles (Waples 1986, in press; M. Slatkin[3]).

That the Channel Islands populations are no more genetically isolated than those at La Jolla was somewhat unexpected, as La Jolla is part of the major mainland metapopulation that includes much of the distributional range of these shore fishes. It was therefore thought that La Jolla samples would show the greatest overall genetic affinity with other localities. Such a pattern was reported by Haldorson (1980), who found allele frequencies in the surfperch *Damalichthys vacca* to be similar in a series of mainland populations but distinctive at Catalina. Furthermore, Tegner and Butler's (1985) study of drift bottles released at the Channel Islands indicated at most 5-10% reach the mainland, suggesting that the amount of genetic exchange may likewise be low.

However, these findings are not inconsistent with the results of the present study when two factors are considered. First, Tegner and Butler's (1985) study was designed to estimate the numerical impact on local green abalone, *Haliotis fulgens*, populations of larvae derived from the Channel Islands. Because relatively few *H. fulgens* larvae appear likely to cross from the Channel Islands to the mainland, it was concluded that the Channel Islands populations cannot be expected to reseed those on the mainland that are locally depleted through overfishing, pollution, destruction of habitat, etc. Although a small percentage (say 5%) of larval exchange may not exert a significant numerical impact on a population, migration at that rate is very high from the perspective of maintaining similar frequencies of neutral alleles. In fact, the exchange of only a few breeding individuals per generation is sufficient to prevent substantial genetic divergence between populations (Spieth 1974).

Second, the Channel Islands populations might well have proved to be relatively more divergent in the present study if additional mainland populations had been included, as was the case in Haldorson's study. Nevertheless, it is noteworthy that Channel Islands populations do not appear to be genetically isolated to any substantial degree. They may thus play a more significant role in the population structure of marine species in this area than had been believed. The consistently strong affinity between Channel Islands and La Jolla populations suggests that the Southern California Eddy may be effective as a means of larval transport between mainland and island localities.

The second major point to emerge from this study is that the population genetic structure of *Caulolatilus princeps* is very different from that of any of the other species. In fact, the pattern of genetic affinity between populations of the ocean whitefish is almost exactly the opposite of the pattern typical of the remaining shore fishes. This result was puzzling at first, as the life history features of this species are not particularly unusual. However, through the aid of H. Geoffrey Moser (National Marine Fisheries Service, La Jolla, CA), we obtained unpublished larval capture data that shed considerable light on this problem. Figure 2 is a plot of these data, collected by CalCOFI sampling programs during 1955-59. In this 5-yr period no *C. princeps* larvae were collected north of central Baja California, Mexico (lat. 30°N). In this respect, the larval distribution of the ocean whitefish is similar to that observed by Kramer and Smith (1973) for the California yellowtail, *Seriola dorsalis* (= *S. lalandi*). In contrast, larvae of the other species in this study for which data are available were frequently taken in the Southern California Bight during 1955-59 (percentage of positive collection localities north of lat. 30°N: *Chromis punctipinnis*, 28%; *G. nigricans*, 44%; *M. californiensis*, 54%; *S. pulcher*, 39%; Waples 1986). In a more extensive survey of larval catches, Moser et al. (1986) confirmed the unusual pattern for the ocean whitefish for years 1954-81 (only 4 of 163 larvae taken north of 30°N, and none taken in the Southern California Bight), and suggested some possible explanations for the southward shift observed in this species. Thus while the southern populations are near the periphery of the range for most study species, it is the northern populations that are far removed from the apparent sources of ocean whitefish larvae.

As we have seen, a significantly nonrandom pattern of genetic affinity among areas or pairs of areas was found when data for *Caulolatilus princeps* were omitted. This result is not entirely unexpected, as removing the most aberrant data in an analysis of this nature will generally result in an improved significance level of the test statistic. On the other hand, such an approach seems justified in this case, as the objectives of this study were to search for generalized patterns of genetic differentiation and to attempt to explain data for anomalous species in

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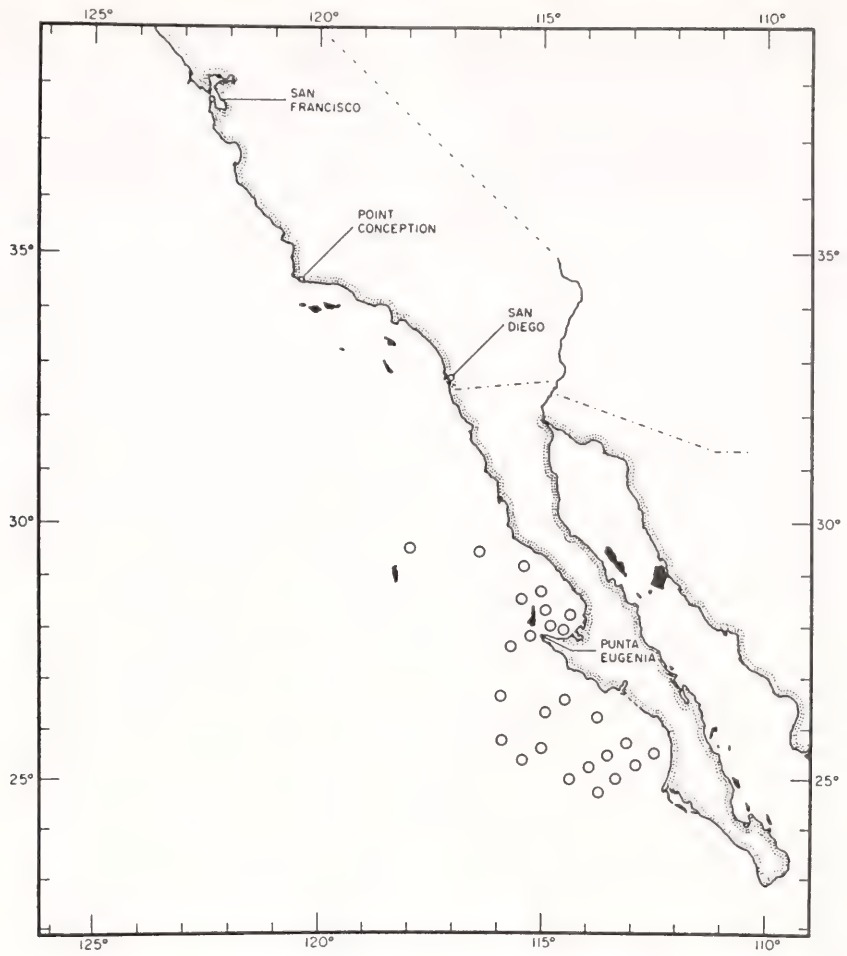

FIGURE 2.—Location of positive collections of *Caulolatilus princeps* larvae taken in CalCOFI sampling program, 1955-59.

terms of life history features. Given the larval capture data discussed above, it is not difficult to understand why the inclusion of data for *C. princeps* tends to obscure patterns of genetic differentiation shared by the other species.

Two other species are exceptions (albeit not as dramatic exceptions as *C. princeps*) to the recurring patterns discussed above. *Girella nigricans* is the only species for which the Channel Islands was found to be the most genetically divergent locality (Table 3), and *S. pulcher* is the only species apart from *C. princeps* for which a strong Punta Eugenia-Guadalupe connection was observed (Table 4). The pattern in *S. pulcher* is due to loci for which consistent heterozygote deficiencies were found (Waples 1986) and thus may provide information that is unrelated to actual levels of gene flow. *Girella nigricans* was the only species to be collected primarily as juveniles; these samples largely comprise a single year class, the allele frequencies for which might be prone to short-term variations. Sampling of juveniles might thus have been expected to yield relatively high levels of genetic divergence, but there was no a priori reason to expect the particular pattern of D values found in this species.

Whether the results for *G. nigricans* are due to as-yet-undetected processes of larval transport or merely random noise in our analysis is thus unclear at present. We face a similar difficulty in explaining the heterogeneity (even among the "core" species) in patterns of genetic affinities between the two northern and two southern populations (Table 4). The decision to include a large number of species in this study mandated a geographically restricted

sampling program, and the resulting analysis provides only a basic outline of these species' population genetic structure. More extensive sampling would no doubt reveal more variations on the patterns identified here. It is likely that such variations would be significantly affected by differences between species in location and timing of spawning. At present, there are neither sufficient inshore hydrographic data nor extensive life history information over the geographic range of most of these species to allow more specific predictions concerning the dynamics of larval drift. Our understanding of the process of larval transport in shallow-water marine organisms can thus be enhanced by more comprehensive sampling programs, involving both genetic and life history analyses.

Nevertheless, it is significant that no major differences in patterns of genetic differentiation could be attributed to dispersal capability per se. Thus of the five "core" species with the most strongly correlated sets of rankings, *E. jacksoni* is a livebearer; *Clinocottus analis* spawns intertidally and has a brief larval life; *P. clathratus and Chromis punctipinnis* have high fecundity and a lengthy larval life; and *M. californiensis* has pelagic juveniles, commonly occurs far offshore with drifting kelp, and thus has the highest dispersal capability of all. This result suggests that the multispecies approach used here may provide information of general use for studying the population biology of other marine organisms (fishes and invertebrates) with pelagic larvae.

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GENETIC ESTIMATES OF STOCK COMPOSITIONS OF 1983 CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, HARVESTS OFF THE WASHINGTON COAST AND THE COLUMBIA RIVER

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ABSTRACT

Allele frequency data for 17 polymorphic protein coding loci from 88 populations of chinook salmon between British Columbia, Canada and California, U.S.A. were used to obtain maximum likelihood estimates of contributing populations to fisheries off the coast of Washington, U.S.A. Data were available for the commercial troll fishery of May 1982 and for commercial, Indian, and sport fisheries during spring and summer 1983. The estimated contributions of fall run fish returning to areas of the lower Columbia River (collectively called "tules") to the May troll fisheries were 76.5% in 1982 and 54.9% in 1983. In contrast, the estimated proportion of fall run fish destined for areas of the upper Columbia River (collectively called "upriver brights") was less than 5% in both years, although these runs are known to make substantial contributions to more northern fisheries of Canada and Alaska. A considerable difference for each year occurred in the estimated proportion of California fish (2.8% in 1982 and 18.7% in 1983).

Differences occurred among the fisheries and areas sampled in 1983. Larger estimates for Canadian and Puget Sound (Washington) fish occurred in fisheries of northern areas; the largest was 41% for the Indian fishery in the Strait of Juan de Fuca. A greater proportion of California fish in any particular area was taken in sport fisheries. The subset of tule populations returning to the Kalama and Cowlitz river drainages was harvested at a higher rate in sport than commercial fisheries. This study demonstrates the capabilities of the involved procedures for generating timely and reliable estimates of stock composition, and serves as a starting point for more detailed understandings of the oceanic distribution of chinook salmon populations.

Chinook salmon, *Oncorhynchus tshawytscha*, runs returning to Pacific drainages of the western United States are a major biological, recreational, and economic resource. Their importance persists in spite of the often excessive harvests, disruptions of habitats, and blockages of migratory routes that have occurred during the past century. The vitality of these runs continues to fluctuate under the influence of many factors. Conflicting demands of multiple user groups, including recreational, commercial, native American, and international fishing interests, tend to stress the overall resource. Water requirements for energy, irrigation, and human consumption often conflict with even minimal conditions for fish rearing, passage, and reproduction. Instabilities of nature in freshwater and marine environments also contribute substantially to fluctuations in growth, migration, and survival.

The management of this resource is further complicated by the ecological and genetic diversity of its individual populations. For instance, fish harvested off the Washington coast represent a complex and continually changing mixture of stocks destined for many areas (Fig. 1; see also Miller et al. 1983). Runs returning to the Columbia River illustrate this diversity; here freshwater entry extends from February through October, and upstream migration distances range from virtually nothing to many hundreds of miles.

The largest numbers of Columbia River chinook salmon return in the fall and consist of two distinct types. Fish of that segment of the run commonly called "brights" retain the silver color of ocean-caught salmon for extended periods following their freshwater entry and return primarily to areas above The Dalles Dam. Brights are largely maintained by natural reproduction with hatchery supplementation of some segments. Fish of the largest segment of the fall run are referred to as "tules"; they approach spawning condition rapidly as soon as, and often before, they enter fresh water. Tules return to areas below The Dalles Dam and are perpetuated almost entirely by hatcheries. Although both tules

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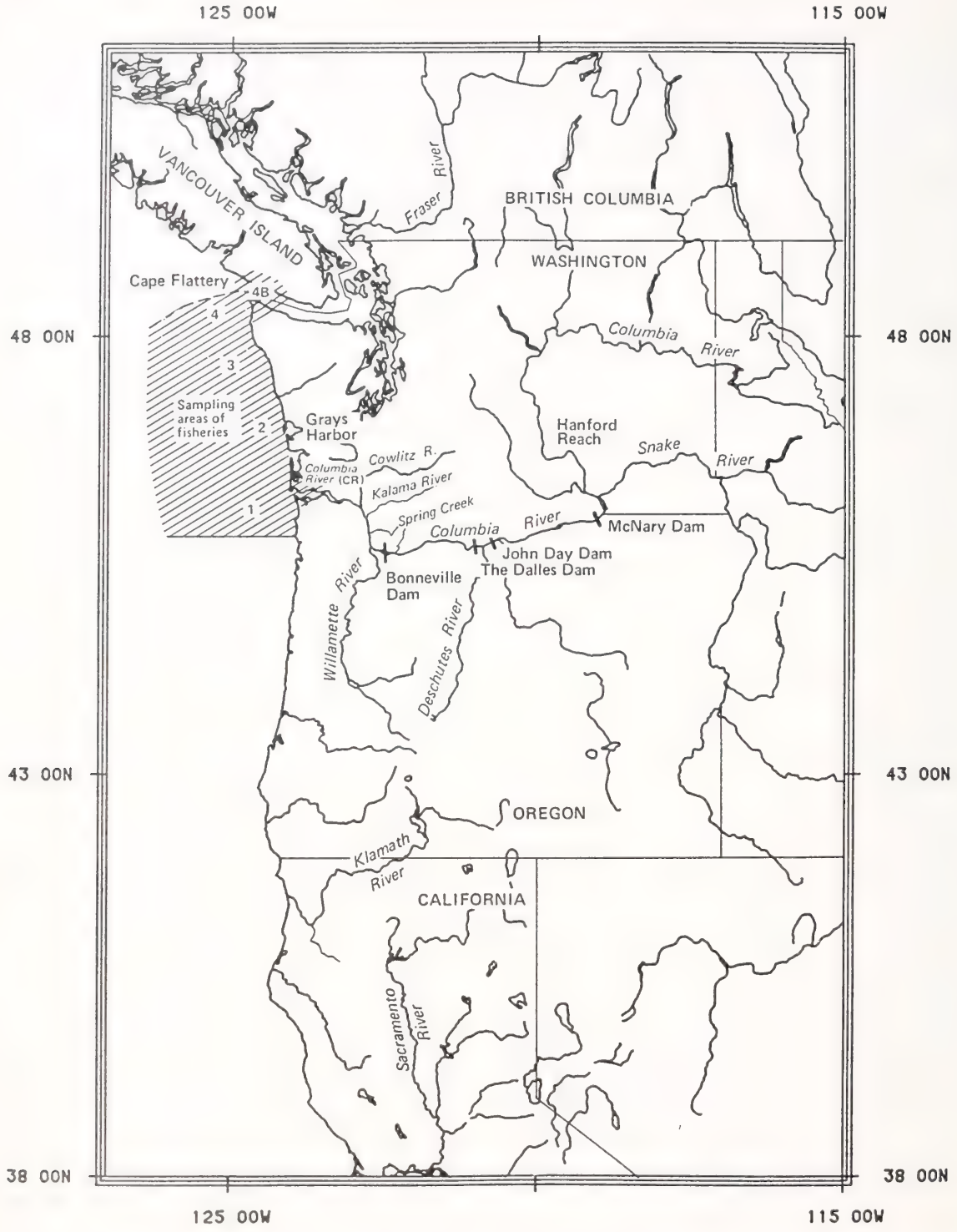

FIGURE 1.—Areas of baseline and mixed stock sampling.

and brights contribute to oceanic fisheries (Pacific Fishery Management Council 1981[3]) the persisting prime condition of brights makes them highly favored in river fisheries.

An ideal program for harvest management of chinook salmon would include the capability of identifying the abundance and distribution of distinct breeding groups (such as component stocks of the tule and bright runs of the Columbia River) in a particular fishery. This capability would permit adjustments of regulations to permit both protection of weaker stocks and more optimal harvest of abundant stocks, depending on their proportions in a fishery. Current information based primarily on data from coded wire tags provides a broad and general overview of hatchery stocks, but lacks details to impose differential harvest regulations adequately and does not yield information on wild populations. In addition, a sufficient number of tags must accumulate in the fishery or in terminal areas before any quantitative interpretation can be made concerning stock distribution. This requirement coupled with the lag time between field collection and tag decoding has precluded in-season regulatory adjustments based on relative stock strengths.

The ability to estimate component stocks in stock mixtures based on genetic profiles of contributing groups has recently been developed and applied (Grant et al. 1980; Fournier et al. 1984; Beacham et al. 1985; Pella and Milner 1987). Numerous estimates of stock mixtures of chinook salmon have been made using a genetic stock identification (GSI) procedure described by Milner et al. (1983). These applications (Miller et al. 1983; Milner et al. 1985) have substantially increased the ability to manage stock mixtures of chinook salmon.

The genetic procedures provide estimates of stock composition with greater detail and precision than has previously been possible when the following two conditions are met. First, known genetic differences (presently identifiable by electrophoretic methods, among other techniques) must exist among populations contributing to a particular stock mixture. Second, a data base of calculated genotypic frequencies (based on a sufficient number of genetic systems) must be developed for those populations that are likely to compose a fishery.

The GSI procedure obtains maximum likelihood estimates of stock composition using the genotypic frequencies of the data base and of the stock mixture. The GSI analysis of the May 1982 troll fishery off the Washington coast using a data base for California through British Columbia provided the most detailed analysis of an oceanic salmon fishery to date (Miller et al. 1983).

This paper follows a general description of the GSI and its application to stock mixtures of salmonids provided in Milner et al. (1985). Estimates of stock composition were obtained from samples collected from fisheries off the Washington coast during the spring and summer of 1983. A particular focus was given to the fall runs of the Columbia River because of the major contributions these runs have historically made to oceanic fisheries. This information is intended to provide managers and biologists with better insights into the life histories of chinook salmon populations in this area of intermingling, and to initiate a continuing record of this species' oceanic distribution and relative abundance.

MATERIALS AND METHODS

The procedures used in this study are outlined below. Many of the details required for specific application are necessarily omitted, but are available in the referenced sources.

Baseline Populations

Data were obtained from 88 collections taken from British Columbia through California and represented distinct breeding units in most cases (Table 1). Intact juveniles or samples of tissues (eye and liver were the tissues of interest in the present study) from adult fish were taken in the field and transported frozen (usually on dry ice) to the laboratory for further processing prior to electrophoresis.

Methods used for detection of electrophotetic variants followed procedures outlined in Utter et al. (1974) and May et al. (1979). The three buffer systems used included:

1) A Tris-boric acid-EDTA gel and tray buffer, pH 8.5 (Markert and Faulhaber 1965).

2) An amine citric acid gel and tray buffer, pH 6.5 (Clayton and Tretiak 1972).

3) A Tris-citric acid-lithium hydroxide-boric acid gel buffer, and a lithium hydroxide-boric acid tray buffer, pH 8.5 (Ridgway et al. 1970).

A system of nomenclature for locus and allelic designations followed Allendorf and Utter (1979).

[3]Pacific Fishery Management Council. 1981. Proposed plan for managing the 1981 salmon fisheries off the coast of California, Oregon, and Washington. Pacific Fishery Management Council, 526 S.W. Mill St., Portland, OR 97201.

TABLE 1.—Geographical area and stock group of the 88 baseline populations used in estimating composition of mixed stock fisheries.

Major geographical district, type of stock, and baseline population[1,2]	Stock group	Total no. examined
Columbia River Basin		
Tule (lower river fall run)	1	150
Spring Creek-Little White Salmon R.-Washougal R.	1a	—
Cowlitz R.-Kalama R.	1b	144
Upriver brights (fall run)	2	
Mid river		
Deschutes R.	2a	49
Priest Rapids-Hanford Reach	2b	249
Snake River		
Ice Harbor	2c	200
Other stocks	3	—
Lower river, fall run		
Lewis R., brights		50
Lower river, spring run		
Cowlitz R.,-Kalama R.		100
Lewis R.		50
Willamette R., spring run		
Eagle Creek-McKenzie R.		88
Hatcheries using stocks of upper river origin, (spring run)		
Little White Salmon*-Carson*-Leavenworth*		148
Mid-Columbia River, spring run		
Klickitat R.		50
Deschutes R., spring run		
Warmsprings*-Round Butte*		109
Upper Columbia River		
Winthrop, spring run		129
Wells Dam, summer run		50
Snake River, spring run		
Rapid R.-Valley Ck.		
Sawtooth Hatchery-Red R.		165
Snake River, summer run		
McCall Hatchery*-Johnson Ck.*		106
California	4	
Sacramento River, fall run		
Coleman (Battle CK.)-Nimbus-Upper Sacramento (late)		300
Feather River-Mokelumne		200
Sacramento River, spring run		
Feather River		50
Klamath River, fall run		
Iron Gate		99
Trinity R.		100
Klamath River, spring run		
Trinity R.		50
Oregon and Washington coast	5	
Oregon, fall run		
Chetco R.		100
Lobster Ck.		50
Elk R.		100
Sixes Estuary*		100
Oregon and Washington coast—*Continued*		
Oregon, fall run—*Continued*		
Coquille Estuary		115
Siuslaw Bay		82
Salmon R.		99
Nestucca R.-Alsea Bay-Siletz R.-Fall Ck.		346
Cedar Ck.*		100
Trask R.-Tillamook R.		188
Nehalem Estuary		141
Oregon, spring run		
Cole R.-Hoot Owl Ck.		163
Rock Ck.		100
Cedar Ck.		99
Trask R.		100
Washington, fall run		
Naselle R.		99
Humptulips R. (early)		50
Quinault R.		100
Queets R.		120
Hoh R.		100
Soleduck		50
Washington, summer run		
Soleduck R.*		100
Washington, spring run		
Soleduck R.		100
Puget Sound and British Columbia	6	
Puget Sound, fall run		
Elwha R.		100
Hood Canal*		98
Deschutes R.		150
Green R.-Samish R.		149
Puget Sound, summer run		
Skykomish R.		100
Skagit R.		100
Puget Sound, spring run		
N. Nooksack R.		50
S. Nooksack R.		50
British Columbia, fall run		
Qualicum*		85
Puntledge*		100
Quinsam*		97
Robertson Ck.		100
Capilano*		99
San Juan R.		50
British Columbia, summer run		
Fraser River		
Tete Jaune		38
Clearwater		45
Chilko R.*		49
Stuart R.*		50
Nechako R.		55
Babine R.*		39

[1]Populations joined by hyphens were not distinguishable based on significant differences of allelic frequencies, and were analyzed as single units.
[2]Asterisks (*) indicate stocks or stock groups excluded from final estimates based on preliminary estimates indicating a contribution of less than 30 fish to total catch of all fisheries sampled (see text).

Multiple loci for the same class of protein are numbered sequentially starting with the locus having the most cathodal activity. Alleles are designated numerically as the percentage of the mobility of the homomeric band of a protein encoded by a variant allele relative to the mobility of the homomeric protein band encoded by the common allele (which is designated 100).

Estimates of allele frequencies were obtained for 17 polymorphic loci from each population sampled. These loci, the conditions for their electrophoretic detection, and the numbers and relative electrophoretic mobilities of their variant allelic forms are outlined in Table 2. The allelic frequencies of these collections for these loci will be presented in a companion publication describing the genetic population

TABLE 2.—Polymorphic enzymes providing genetic information for baseline populations and stock mixtures. Tissue used were eye (E), and liver (L). Explanations for locus and allele designations and for buffers are given in text.

Enzyme (enzyme commission no.)	Locus designation (variante alleles)	Tissue	Buffer
Aconitate hydratase (4.2.1.3)	Ah-4(69,86,108,116)	L	2
Adenosine deaminase (3.5.4.4)	Ada-1(83)	E	1
Aspartate aminotransferase (2.6.1.1)	Aat-3(90)	E	1
Dipeptidase (glycyl-L-leucine) (3.4.13.11)	Dpep-1(90)	E,L	1
Glucose-6-phosphate isomerase (5.3.1.9)	Gpi-3 (93,105)	E,L	3
Glutathione reductase (1.6.4.2)	Gr-1(85)	E,L	1
Hydroxyacylglutathione hydrolase (3.1.2.6)	Hagh(140)	L	1
Isocitrate dehydrogenase (1.1.1.42)	Idh-3,4(50,74,127,142)	E,L	2
Lactate dehydrogenase (1.1.1.27)	Ldh-4(71,134)	E,L	3
	Ldh-5(70,90)	E	1
Malate dehydrogenase (1.1.1.37)	Mdh-1,2(27, – 45,146)	E,L	2
	Mdh-3,4(70,83,121)	E,L	2
Mannose-6-phosphate isomerase (5.3.1.8)	Mpi(95,109,113)	E,L	1
Phosphoglucomutase (5.4.2.2)	Pgm-1(– 70, – 84)	E,L	2
Phosphoglycerate kinase (2.7.2.3)	Pgk-2(90)	E,L	2
Superoxide dismutase (1.15.1.1)	Sod-1(– 260,560,1250)	L	1
Tripeptide aminopeptidase (L-leucylglycylglycine) (3.4.11.4)	Tapep(45,130)	E,L	3

structure of North American chinook salmon stocks. The general locations of baseline samples and mixed fisheries are outlined in Figure 1.

The data base of six major groupings used to analyze the ocean fisheries was derived from the data of the 88 collections as follows: 1) Contingency tests were used to combine data for populations lacking significant allelic differences, thus reducing the number of groups to 65. 2) GSI estimates were made from weighted (by catch) samples of genotypic data from each fishery; based on this information, those groups estimated by maximum likelihood (see below and Milner et al. 1983[4]) to contribute less than 0.034% (30 fish) to the total catch of all fisheries sampled were eliminated. This brought the number of groups down to 50. 3) Estimates made for each of the 50 groups were combined into the six major groupings of Table 1 to permit a particular focus on tule and upriver bright stocks in the Columbia River.

Estimates of the composition of the 1 September gill net fishery in the Columbia River were obtained for each of the 11 Columbia River fall run collections and combined as indicated in Table 1.

Population Mixtures

Almost all of the ocean sampling was done at port of landing. Eye fluid, the only tissue, was collected in tubes placed on chipped ice, stored in various freezers, and shipped weekly in a portable freezer to the laboratory where storage was at $-90°C$ until preparation for electrophoresis. The September gill net fishery was sampled for livers only. Samples obtained by Washington Department of Fisheries (WDF) personnel from fish buyers in Ilwaco and Chinook, WA, and Astoria, OR, were collected and shipped on dry ice, and electrophoresis was carried out immediately following their arrival.

Electrophoretic data were collected only for those polymorphic loci that were expressed in the collected tissues:

[4]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study. Unpubl. rep., 66 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112. (Final Report of Research to Bonneville Power Administration, Agreement DE-A179-82BP28044M001.)

eye — Aat-3; Ada-1; Dpep-1; Gpi-3; Gr-1; Idh-3,4; Ldh-4; Ldh-5; Tapep; Mdh-1,2; Mdh-3,4; Pgm-1; Pgk-2; Mpi.

liver — Ah-4; Dpep-1; Hagh; Gpi-3; Gr-1; Idh-3,4; Tapep; Ldh-4; Mdh-1,2; Mdh-3,4; Pgm-1; Pgk-2; Mpi; Sod-1 (Table 2).

Mixed Fishery Analysis

Maximum likelihood estimates of proportionate contributions of baseline populations to different population mixtures were obtained by the procedures described in Milner et al. (fn. 4). Through an iterative procedure (the EM algorithm, Dempster et al. 1977), the estimates are obtained using the frequencies of genotypes in the mixtures and in the baseline populations. Standard deviations of indiviual and pooled estimates were based on an asymptotic variance as described in Milner et al. (fn. 4). These variances were found to be consistently higher than empirically derived variances within the sample sizes of the present study (Milner et al. fn. 4). The geographic range of mixed fisheries sampled in this study was from the Strait of Juan de Fuca southward through the mouth of the Columbia River to the northern coast of Oregon (Fig. 1).

TABLE 3.—Estimated proportions of stock groups and subgroups in fisheries of 1983.

Fishery class[1]	area[2]	month[3]	Stock group (Estimated contribution and in parentheses standard deviation)									Number in sample [fishery]
			1a	1b	2a	2b	2c	3	4	5	6	
C	1	5	0.350	0.130	0.009	0.010	0.008	0.147	0.049	0.092	0.202	1,243
			(0.022)	(0.020)	(0.042)	(0.036)	(0.038)	(0.034)	(0.052)	(0.079)	(0.037)	[10,870]
	2		0.393	0.228	0.010	0.001	0.002	0.100	0.019	0.080	0.187	2,050
			(0.044)	(0.047)	(0.052)	(0.021)	(0.069)	(0.041)	(0.101)	(0.101)	(0.055)	[23,780]
	3		0.456	0.054	0.022	0.004	0.009	0.168	0.124	0.042	0.122	319
			(0.183)	(0.187)	(0.488)	(0.282)	(0.523)	(0.314)	(0.471)	(0.873)	(0.449)	[1,600]
	4		0.375	0.054	0.007	0.003	0.004	0.133	0.189	0.081	0.153	600
			(0.076)	(0.111)	(0.212)	(0.112)	(0.255)	(0.098)	(0.385)	(0.430)	(0.226)	[4,062]
	1-4		0.362	0.187	0.013	0.001	0.004	0.121	0.047	0.079	0.187	3,475
			(0.002)	(0.003)	(0.005)	(0.007)	(0.009)	(0.007)	(0.010)	(0.007)	(0.004)	[40,314]
	2	7	0.515	0.156	0.014	0.001	0.011	0.123	0.035	0.047	0.101	1,044
			(0.068)	(0.073)	(0.180)	(0.120)	(0.195)	(0.090)	(0.296)	(0.263)	(0.114)	[4,965]
	3		0.225	0.214	0.032	0.000	0.012	0.069	0.115	0.191	0.142	784
			(0.060)	(0.104)	(0.161)	(0.105)	(0.166)	(0.140)	(0.109)	(0.287)	(0.162)	[3,511]
	4		0.341	0.078	0.016	0.013	0.016	0.101	0.160	0.148	0.126	1,243
			(0.045)	(0.066)	(0.111)	(0.071)	(0.123)	(0.075)	(0.093)	(0.195)	(0.099)	[5,739]
	2-4		0.353	0.143	0.019	0.007	0.026	0.111	0.087	0.133	0.121	2,989
			(0.032)	(0.039)	(0.074)	(0.037)	(0.069)	(0.047)	(0.046)	(0.104)	(0.060)	[14,214]
	1-4	5-7	0.366	0.187	0.014	0.001	0.006	0.101	0.056	0.090	0.181	4,701
			(0.001)	(0.001)	(0.004)	(0.003)	(0.005)	(0.003)	(0.005)	(0.006)	(0.003)	[54,527]
I	3-4		0.298	0.197	0.021	0.002	0.019	0.163	0.126	0.061	0.114	462
			(0.113)	(0.129)	(0.391)	(0.246)	(0.304)	(0.149)	(0.161)	(0.622)	(0.261)	[3,923]
	4a		0.357	0.054	0.003	0.002	0.003	0.076	0.409	0.022	0.082	428
			(0.095)	(0.125)	(0.477)	(0.226)	(0.277)	(0.166)	(0.426)	(0.663)	(0.358)	[2,283]
	3-4a		0.330	0.115	0.012	0.003	0.008	0.171	0.221	0.032	0.109	731
			(0.064)	(0.082)	(0.259)	(0.130)	(0.243)	(0.098)	(0.448)	(0.409)	(0.202)	[6,206]
S	1-2	6	0.218	0.158	0.011	0.000	0.015	0.085	0.014	0.099	0.399	1,633
			(0.045)	(0.060)	(0.128)	(0.076)	(0.124)	(0.093)	(0.147)	(0.177)	(0.092)	[13,232]
	1	6-7	0.202	0.266	0.017	0.001	0.010	0.125	0.029	0.079	0.271	1,530
			(0.007)	(0.010)	(0.028)	(0.016)	(0.024)	(0.018)	(0.032)	(0.063)	(0.024)	[9,581]
	2		0.294	0.215	0.005	0.000	0.006	0.099	0.037	0.114	0.228	1,760
			(0.008)	(0.017)	(0.031)	(0.013)	(0.033)	(0.024)	(0.044)	(0.047)	(0.015)	[15,522]
	1-2		0.247	0.263	0.008	0.000	0.009	0.122	0.046	0.107	0.198	2,846
			(0.006)	(0.007)	(0.014)	(0.007)	(0.016)	(0.010)	(0.018)	(0.023)	(0.007)	[25,103]
		7-8	0.326	0.217	0.014	0.000	0.011	0.048	0.069	0.070	0.232	368
			(0.165)	(0.238)	(0.849)	(0.780)	(0.563)	(0.548)	(0.981)	(1.58)	(0.747)	[2,483]
		8-9	0.240	0.228	0.009	0.047	0.040	0.057	0.088	0.137	0.155	739
			(0.076)	(0.110)	(0.304)	(0.205)	(0.251)	(0.146)	(0.435)	(0.517)	(0.206)	[6,066]
		5-9	0.251	0.211	0.007	0.001	0.013	0.118	0.044	0.096	0.259	5,315
			(0.001)	(0.002)	(0.004)	(0.003)	(0.005)	(0.003)	(0.008)	(0.007)	(0.003)	[46,884]
C	CR	9	0.780	0.146	0.011	0.052	0.007	0.004	—	—	—	2,040
			(<0.001)	(0.001)	(0.001)	(<0.001)	(<0.001)	(<0.001)				[15,668]

[1]C = commercial, I = Indian, S = Sport.
[2]Areas are as indicated in Figure 1.
[3]In sport fishery, dates for month are 6 = 5-29 – 6-17, 7 = 6-18 – 7-29, 9 = 8-16 – 9-11; in Columbia River commercial fishery 9 = 9-1 only.

DISTRIBUTIONS OF STOCK GROUPS IN OCEAN FISHERIES

Estimated contributions to different fisheries by the two tule and three upriver bright subgroups, and by the four other geographic groupings, are listed in Table 3. Some of the major features of Table 3 are graphically projected in Figure 2. A stock structure that varies with regard to both time and area is evident.

Some consistency over time is seen in comparisons of the May and July commercial troll catches in sampling areas 2 and 4. Notable features in sampling area 2 include the overall predominance of the tule stocks and a minimal contribution of Puget Sound and Canadian fish. Sampling area 4 has a smaller tule contribution and a substantially larger proportion of Puget Sound and Canadian fish.

Although comparisons of the sport and commercial fisheries are limited by somewhat different sampling areas, a greater proportion of California fish is taken in the sport fisheries. This is seen particularly in the early fishery. More intense sampling in area 1 may account for some of the early differences, but the data of Table 3 suggest a persistent trend even in common times and sampling areas.

The Indian troll fishery provided the only information from sampling area 4B. The most distinctive feature of this fishery was the high proportion (41%) of the Puget Sound and Canadian group. This figure was more than double the estimated contribution of this group in any other fishery.

The ocean fisheries off the Washington coast are notable for the usually negligible representation of upriver bright stocks. The highest estimated contribution (9.6%) occurred in the sport fishery of 16 August-11 September which was the largest fishery sampled. The timing and distribution of upriver bright fish will be considered in greater detail below.

Estimated distributions for the May 1982 and 1983 troll fisheries were compared (Table 4), reveal-

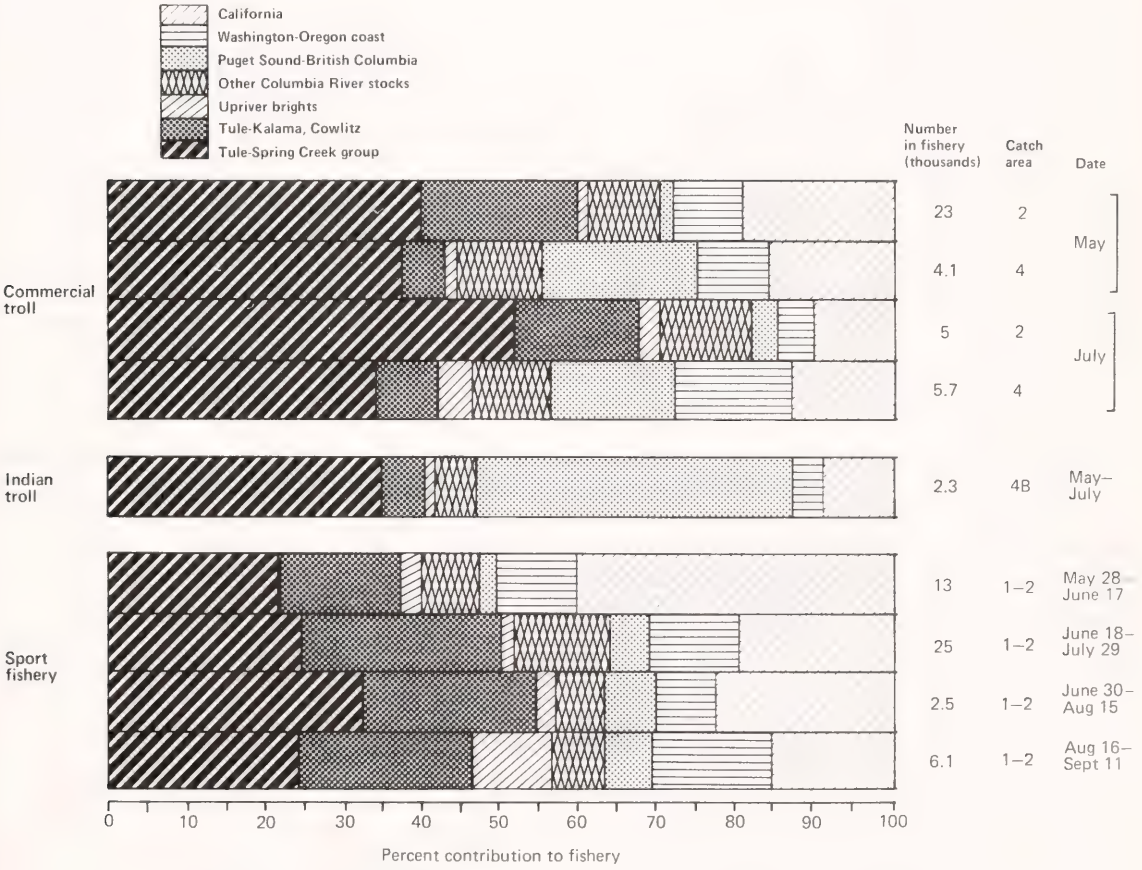

FIGURE 2.—Estimated contributions of seven stock groups in different ocean fisheries.

TABLE 4.—Comparisons of estimated percentage stock group contributions to May troll fisheries of 1982 and 1983 within sampling areas 1 and 4 and 1 through 4.

	Percentage catch estimated from sampling area					
	1		4		1 through 4	
Stock group	1982 (1,414)[2]	1983 (1,243)	1982 (448)	1983 (600)	1982[1] (2,504)	1983 (3,475)
Columbia River						
Tule	78.2	48.2	45.6	42.9	76.5	54.9
Upriver bright	4.0	2.7	8.8	1.0	4.3	1.8
All groups	88.9	65.6	56.8	57.6	90.9	69.5
California	5.3	20.2	4.4	15.3	2.8	18.3
Oregon-Washington coast	3.8	9.2	9.7	8.1	2.9	7.9
Puget Sound-Canada	1.9	4.9	29.2	18.9	3.4	4.7

[1]Data from Miller et al. 1983.
[2]Values in parentheses designate number of fish sampled.

ing considerable dissimilarity as well as some consistency. A much larger proportion of tules and a correspondingly smaller contribution of California fish was seen in 1982 in sampling areas 1 through 4.

The comparisons of estimates within sampling areas 1 and 4 differed between both sampling areas and years. For each year, estimates within sampling area 1 were similar to the estimates based on the total sample. Estimates from sampling area 4 were consistent with those of the total sample but with a larger proportion of California fish estimated in 1983 and substantially larger Puget Sound-Canadian stock group and smaller tule estimates. These observations are consistent with the location of sampling area 4 at the southern point of entry for most of the populations destined for Puget Sound and British Columbia, and are reinforced by the high proportion of fish estimated for this stock group in sampling area 4B.

The much higher total harvest of the 1982 May troll fishery (73,196; Miller et al. 1983) than in the same fishery for 1983 (40,312) accentuates the difference in numbers of tules taken (approximately 56,000 vs. 22,700).

The numbers of tule group fish returning to the mouth of the Columbia River and to hatcheries (i.e., spawning escapement) were also much lower in 1983 (Washington Department of Fisheries 1984[5]) and were insufficient to fulfill hatchery requirements. This contrast was attributed to a climatological phenomenon termed "El Niño" that affected the oceanic distribution and survival of many species beginning in 1983 (Mysak 1986).

[5]Washington Department of Fisheries. 1984. Status of fall chinook stocks in the northern Oregon through Vancouver Island ocean fishing areas. Unpubl. rep., 35 p. Department of Salmon Harvest Management, Washington Department of Fisheries, 115 General Administration Building, Olympia, WA 98504.

DISTRIBUTION AND RELATIVE CONTRIBUTIONS OF TULES AND UPRIVER BRIGHTS

The actual and potential value of tule and upriver bright runs in the sampling areas of this study warrant a more detailed focus on the abundance of these stocks and their subgroups. The great value of tule stocks in ocean fisheries off the Washington coast has been demonstrated from these and other data (e.g., Miller et al. 1983). Although a similar value for upriver brights in either oceanic or river harvests is not yet apparent, it is premature to assign a lesser value to these runs because of geographic and temporal limitations of sampling. Indeed, data from coded wire tags (Table 5) indicate a distinctly different oceanic distribution of tules and upriver brights. Over half of the recoveries of the tagged fish from the tule stock (Spring Creek) were harvested off the Washington coast. However, only about 5% of the tagged fish from upriver bright stocks were recovered in this area, with over 90% harvested in waters of Alaska and British Columbia.

The substantially increased contribution of upriver brights in the late sport fishery (Table 3, Fig. 2) is consistent with a late migratory surge of these fish. Clearly, based on distributions indicated through tag data in Table 5, the upriver brights contribute heavily to fisheries in areas north of those sampled in this study. However, they were estimated at sizable numbers only very late in this study presumably enroute through the areas sampled to their spawning grounds.

The tules and upriver brights have been considered as unit populations to this point. The subgroup data indicate considerable heterogeneity within both groups with regard to time, area, and fishery. Comparisons of the two tule subgroups (Table 3, Fig. 2) indicate a considerable difference

TABLE 5.—Summary of distribution of oceanic coded wire tag recoveries (N) of 1975 brood year fall chinook salmon from the Snake River, and Priest Rapids and Spring Creek hatcheries.

Source and type of stock	Sample size	Recovery area: Alaska	Canada (B.C.)	Washington	Oregon	Total no. fish
Snake River[1] (upriver bright)	N	176	272	21	11	480
	%	36.7	56.7	4.3	2.3	
Priest Rapids[2] (upriver bright)	N	1,314	1,597	171	13	3,095
	%	42.4	51.9	5.4	0.3	
Spring Creek[2] (tule)	N	0	984	1,319	147	2,450
	%	0	40.2	53.8	6.0	

[1]Data from L. Gilbreath, Northwest and Alaska Fisheries Center, Seattle WA 98112, pers. commun. September 1984.
[2]Data obtained from Pacific Marine Fisheries Commission in 1983.

in their relative frequencies. In both May and July, the proportion of the Cowlitz-Kalama subgroup (group 1b) to the overall tule contribution in the commercial fisheries was considerably higher in sampling area 2 (average 30%) than in sampling area 4 (average 16%). The proportion of this subgroup was highest in the sport fisheries, approaching equality (46%) with the Spring Creek subgroup (1a) in the overall data set and predominating in the June-July fisheries (52%). The Spring Creek subgroup strongly predominated in the tule catch of the river fishery of 1 September (84%, Table 3).

The relative contributions of the three upriver bright subgroups vary considerably in the ocean fisheries (Table 3, Fig. 3). The most notable feature is the absence or negligible contribution of the Priest Rapids subgroup (2b) in all but the last ocean fishery that was sampled, where this subgroup contributes a substantial proportion (49%) of the total estimated upriver bright harvest. This finding was unexpected because this subgroup is by far the largest contributor to the overall upriver bright production (Pattillo and McIsaac 1982). The data of the 1 September river fishery are more consistent with expectations, with 83% of the upriver bright catch estimated to be from the Priest Rapids subgroup. The low estimated contribution of this subgroup to ocean fisheries cannot be explained by the large standard deviations accompanying most estimates because the more precise pooled estimates (Table 3) also indicate a small Priest Rapids contribution.

MANAGEMENT CONSIDERATIONS

The difference in relative proportions of the two tule groups, based largely on class of fishery and

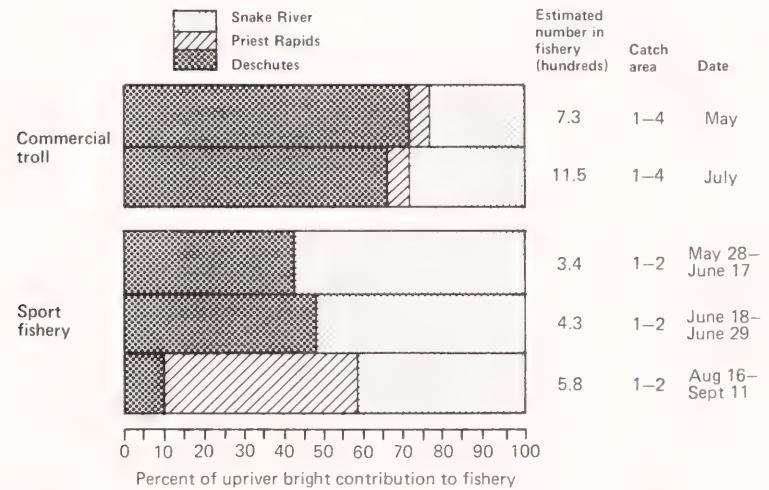

FIGURE 3.—Estimated proportions of three upriver bright stocks to different ocean fisheries.

area, has implications for management. The higher representation of the Cowlitz-Kalama subgroup in the sport fisheries than in the troll fisheries of common times and areas suggests a greater susceptibility of this subgroup to sport harvests. In addition, the relative abundance of the Cowlitz-Kalama subgroup compared with the Spring Creek subgroup was higher in more southern areas for both commercial and sport fisheries. If these trends continue to be observed, different management strategies could be applied for these groups when warranted.

The low estimates of the Priest Rapids subgroup of upriver brights relative to the two less abundant subgroups suggest different oceanic distributions of these subgroups. However, the coded wire tagging data (Table 5) indicate that at least the Snake River and Priest Rapids subgroups are harvested much more intensely in areas to the north of those sampled in this study (no tagging data were available for the Deschutes subgroup). Any attempts to identify and protect the weaker subgroups within the sampling areas of this study would be futile unless similar efforts could be applied to these much larger catches in more northern areas.

A general occurrence of larger proportions of Puget Sound and Canadian fish in the northern sampling areas is suggested by the similar observations for 2 consecutive years and by the particularly high estimates for these fish in area 4B. Since 1983, more detailed GSI estimates from area 4B have, in fact, been used by the WDF to monitor and regulate chinook salmon fisheries in the Strait of Juan de Fuca and Puget Sound areas.

Preliminary results from the September gill net fishery in the lower Columbia River (based on a subsampling of 500 fish) were available on the day following the collection of the samples. This potential for rapid turnaround time increases the value of the GSI as a management tool by permitting inseason regulatory adjustments. Such information would allow greater harvest of a healthy stock while continuing to provide for maximum protection of a depressed stock. For example, in years when bright fish are expected to return in great abundance and tules in low abundance, the GSI method could be used to monitor extended fall gill net fisheries to time the entry of tules. When ratios of tules to brights became unfavorable, fisheries could be curtailed.

It is important to emphasize the arbitrary nature of many of this study's groupings, which were necessary to provide a manageable basis for reporting. A focus on the tule and upriver bright contributions was appropriate because of the extensive baseline data from the Columbia River drainage, the dominance of the tule runs in ocean fisheries, and the distinct oceanic distributions of the tule and upriver bright groups. However, a similar focus on other groupings (e.g., Columbia River spring runs or wild and hatchery stocks of the Oregon coast) is equally feasible, and could easily provide a basis for more detailed information on the distributions of individual populations within such groups.

The completeness and the reliability of the sets of baseline data that are used affects the accuracy of GSI estimates. This study's focus on the contribution of Columbia River populations to stock mixtures in ocean areas adjacent to the mouth of the Columbia River was appropriate for the sets of baseline data that were used. Most estimates were obtained through a data base that included most of the major contributing groups within the Columbia River and allele frequency data from 17 polymorphic loci. These same baseline data can be used over successive years, providing the allele frequencies remain stable among year classes and over succeeding generations. Such stability has been observed for some loci and populations of anadromous salmonids (e.g., Utter et al. 1980; Grant et al. 1980; Altukhov 1981).

This temptation to regard the present baseline data as a static entity should nevertheless be resisted for a number of reasons. Gene flow, genetic drift, and selection could modify allelic frequencies over extended time periods; thus, periodic updating of previously sampled populations is desirable. Temporal changes in allele frequencies of chinook salmon have been reported (Carl and Healey 1984; Kristiansson and McIntyre 1976). The extensive stock transplantations of chinook salmon within the Columbia River make the possibility of gene flow particularly likely for the focal populations of this study. Hatchery populations perpetuated by limited numbers of breeders are particularly susceptible to allele frequency changes through genetic drift (Allendorf and Ryman 1987). Previously unsampled baseline populations should be added, particularly in areas where limited sampling has occurred, to increase the accuracy and broaden the usable range of analyses. The discriminatory powers of GSI analyses are substantially increased as new variable loci are added (see Milner et al. fn. 4). The continuing search for additional markers requires collection of electrophoretic data from previously sampled populations for each new variable locus that is found.

Increasing application of procedures used in this study seems virtually inevitable in view of the per-

sistent need to understand the composition of stock mixtures of salmonids (and other structured groups) better. The obvious management potential of such uses is matched by increased understanding of population structuring and of migratory behavior that will emerge as information accumulates.

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ON THE STANDARD METABOLIC RATES OF TROPICAL TUNAS, INCLUDING THE EFFECT OF BODY SIZE AND ACUTE TEMPERATURE CHANGE

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ABSTRACT

The standard metabolic rates (SMR's) of fishes and the effect of body weight on SMR's are important input parameters to energetics, growth, and population models. This study was undertaken to obtain these data for the tropical tuna species, yellowfin tuna, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*. These data compliment similar SMR measurements from skipjack tuna, *Katsuwonus pelamis*, previously published. The effect of acute temperature change on the SMR of all three species was also determined.

The SMR was estimated by directly measuring the oxygen uptake rate of animals paralyzed with a neuromuscular blocking drug, rather than by the more commonly used method of extrapolation of swimming speed-metabolic rate curves back to zero swimming speed. To test the adequacy of this technique, the SMR's of aholehole, *Kuhlia sandvicensis*, and rainbow trout, *Salmo gairdnerii*, were determined using similar methodology. The SMR's measured in this way were not significantly different from the published SMR's of these species determined by extrapolation of swimming speed-metabolic rate curves back to zero swimming speed.

All three tuna species have very high SMR's, over five times higher than other active teleost species such as salmon and trout. The effect of body size on the SMR is similar in all three tuna species, but the weight specific SMR of tuna decreases more rapidly with increasing body size than in other fishes. Based on SMR's measured at 20° and 25°C, the Q_{10}'s were 3.16, 2.31, and 2.44 for yellowfin tuna, kawakawa, and skipjack tuna, respectively. These are similar to Q_{10} values found for the SMR's of other teleosts.

Tunas can achieve exceptionally high maximum aerobic metabolic rates. This ability requires a complete set of anatomical, physiological, and biochemical adaptations. I hypothesize that one of these adaptations, large gill surface areas, causes tunas to have exceptionally high energy demands even at rest. Tunas' high SMR's are an inevitable consequence of their ability to achieve exceptionally high maximum aerobic metabolic rates.

The standard metabolic rate (SMR) (the metabolic rate of a postabsorptive animal completely at rest) and the effect of body size on SMR are important input parameters to growth, energetics, and population models (e.g., Sharp and Francis 1976; Kitchell et al. 1978). This study was therefore undertaken to obtain these data for yellowfin tuna, *Thunnus albacares*, and kawakawa, *Euthynnus affinis*. These measurements were designed to directly compliment the SMR measurements for skipjack tuna, *Katsuwonus pelamis*, that had been previously published (Brill 1979). The effect of acute temperature change on the SMR of skipjack tuna, yellowfin tuna, and kawakawa was also determined. The effect of acute temperature change, as opposed to the effect of temperature adaptation, is relevant to tuna because of the 5° to 15°C water temperature changes these species normally experience during the daily vertical movements which are a constant feature of their behavior in the open ocean (Dizon et al. 1978; Carey and Olson 1982; Yonemori 1982).

In other teleosts, SMR's have been determined by extrapolating metabolic rate-swimming speed curves back to zero swimming speed (e.g., Brett 1965). Although Graham and Laurs (1982) have successfully measured the metabolic rate of albacore, *T. alalunga*, (a temperate tuna species) swimming in a water tunnel, this methodology is presently not possible with tropical tunas (skipjack tuna, yellowfin tuna, and kawakawa). Attempts to get these species to swim in several prototype water tunnel designs have shown that they will do so for only very short periods (Brill and Dizon 1979 and unpublished observations). As a result, measuring the SMR's of tropical tunas directly in animals paralyzed with a neuromuscular blocking agent is currently the only method available to obtain these data.

To validate this technique, the SMR's of rainbow

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trout, *Salmo gairdneri*, and aholehole, *Kuhlia sandvicensis*, were also measured using paralyzed animals. These two species were chosen because they are available in Hawaii and because there are published data on their SMR's based on extrapolation of swimming speed-metabolic rate curves back to zero swimming speed (Muir et al. 1965; Bushnell et al. 1984).

The SMR of a 1 kg skipjack tuna (412 mg O_2/h, Brill 1979), is almost five times greater than that of a 1 kg sockeye salmon, *Oncorhynchus nerka* (83 mg O_2/h, Brett and Glass 1973). The former measurements were made at 25°C and the latter at 20°C, because 25°C is the upper lethal temperature for salmon (Brett 1972). However, a 5°C temperature difference could not account for this SMR difference because the Q_{10}'s for the SMR's of fishes are generally about 2 (Robinson et al. 1983). The maximum sustainable aerobic metabolic rate (MMR, the metabolic rate at the maximum swimming speed sustainable for at least 1 h) of a 1 kg sockeye salmon at 20°C is 796 mg O_2/(kg·h), whereas 1.8-2.2 kg skipjack tuna at 24°C have been shown to be able to achieve active metabolic rates over 2,000 mg O_2/(kg·h) (Gooding et al. 1981). Although there are no metabolic rate measurements available for tunas at their maximum sustainable swimming speeds, two conclusions are still obvious: 1) skipjack tuna have very high SMR's even when compared with other active equal sized teleosts and 2) skipjack tuna are capable of very high aerobic metabolic rates.

I hypothesize that the high SMR's of tunas are primarily a result of their large gill surface areas (Hughes 1979). In other words, adaptations that permit high maximum sustainable rates of oxygen uptake (i.e., high MMR's) obligate tunas to have high SMR's. Analogous arguments with respect to the resting and maximal metabolic rates of terrestrial vertebrates have been presented by Bennett and Ruben (1979).

MATERIALS AND METHODS

SMR Measurements-Tuna

Live skipjack tuna, yellowfin tuna, and kawakawa were purchased from local fishermen and maintained at the Kewalo Research Facility (Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA). Animal procurement, handling, and maintenance procedures at this facility are described by Nakamura (1972), Queenth and Brill,[2] and Chang et al.[3] Fishes were maintained in outdoor tanks for a few days to over 1 yr before use. Temperature of the seawater supplied to the holding tanks was 25°C (±2). Food was presented daily; however, individuals were not fed for at least 20 h prior to use in an experiment. This allowed sufficient time for gut clearance and for blood glucose level to return to prefeeding levels (Magnuson 1969).

Each experimental animal was removed from its holding tank by dip net and injected intramuscularly with 1-3 mg/kg of the neuromuscular blocking agent Flaxedil[4] (gallamine triethiodide). The animal was quickly returned to its holding tank, and when it could no longer swim, it was immediately rushed into the laboratory and placed in a Plexiglas flow-through box respirometer similar to that used by Stevens (1972). The respirometer was equipped with a movable partition which was placed immediately behind the fish to reduce the respirometer's volume and, thus, reduce the lag time between actual and measured changes in metabolic rate to only minutes (Niimi 1978). Water flow through the respirometer was maintained at 3-7 L/(kg·min) and was measured every 30-60 min by recording the time to fill a 1 L graduated cylinder. Water temperature was controlled by a chiller and freshwater heat exchanger and by a quartz heater mounted in the inflow seawater line. Temperature control was ±0.3°C.

Unlike the previous study on the SMR of skipjack tuna (Brill 1979), the spinal cord was not cut to stop all overt muscular activity. Rather, an 18-gauge hypodermic needle was placed intramuscularly and connected to the outside of the respirometer via a short length of polyethylene tubing. Through this tube, 0.1-0.3 mL doses of Flaxedil were administered when the fish began to show any slight tail movements. To monitor heart rate, electrocardiogram leads were mounted subcutaneously on the ventral body surface. Heart rate was determined by timing the interval between successive beats with a Hewlett-Packard (HP) 5308A frequency counter. Thermistors were used to measure fish muscle and water temperatures. With the aid of an 18-gauge hypodermic needle, a thermistor bead mounted in 0.9 mm diameter polyethylene tubing was inserted

[2]Queenth, M. K. K., and R. W. Brill. 1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396, Administrative Report H-83-7, 16 p.

[3]Chang, R. K. C., R. W. Brill, and H. O. Yoshida. 1983. The Kewalo Research Facility, 1958 to 1983—25 years of progress. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96822-2396, Administrative Report H-83-14, 28 p.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

into the red muscle immediately adjacent to the spinal column. Thermistor probes were also mounted in the incoming seawater line and in the respirometer box itself. Red muscle and water temperatures were determined by measuring the resistance of the various thermistors with an HP 3456A digital multimeter.

Oxygen concentration (milligrams per liter) of the water upstream and downstream of the fish was determined with a dissolved oxygen meter (Yellowsprings Instrument, model 51A) equipped with a Clark-type polarographic electrode oxygen-temperature probe. The probe was normally in the outflow seawater line, but was moved to the inflow seawater line to determine inflow seawater oxygen levels every 30-60 min. The analog output of the oxygen meter was also measured with the HP digital multimeter. An HP 9825A computer was used to control an HP 5930A six-channel relay actuator which permitted the digital multimeter to determine sequentially the resistances of various thermistors and the analog output of the oxygen meter. Seawater oxygen level, red muscle and water temperatures, metabolic rate, and heart rate were calculated and printed by the computer at 5-min intervals.

After being sealed, the respirometer box was covered with black plastic to minimize disturbance to the fish. Temperature of the seawater supplied to the respirometer was maintained at 21°-22°C for the first 1-2 h because reduced water temperature has been shown to help tuna survive after handling (Barrett and Connor 1964). Seawater temperature was then changed to either 20° or 25°C, and the fish maintained at the test temperature until its metabolic rate remained relatively stable for at least 1 h. The SMR was estimated by averaging the last 5-12 metabolic rate measurements. The standard deviations of the metabolic rate measurements used to estimate SMR were <11% of the mean (i.e., SMR) in all cases, and in 70% of the cases, the standard deviations were <5% of the mean.

To determine the SMR at a second temperature, the water temperature was changed to either 20°, 25°, or 30°C, and metabolic rate measurements continued again until the fish's metabolic rate remained stable for 1 h.

SMR Measurements-Aholehole and Rainbow Trout

Aholehole were obtained from Sea Life Park (Waimanalo, HI) and rainbow trout from a commercial fish farmer (through the University of Hawaii, Hilo). The former were maintained in an outdoor tank with running seawater at 25°C (±2) and the latter, in an indoor tank with running freshwater at 15°C (±2). Both species were fed daily, but individuals were not fed for at least 20 h prior to use in an experiment.

The respirometer used for aholehole was essentially identical to that used by Davis and Cameron (1971) and Jones and Schwarzfeld (1974) to measure water flow and gas exchange across the gills of rainbow trout. The aholehole were anesthetized in 1:10,000-1:30,000 MS222 (Tricaine methanosulfonate). A thin, rubber membrane was sutured around the fish's mouth and sealed with a small amount of tissue glue (Histoacryl, B. Braun Melsungen AG, West Germany). The fish was then placed in a black Plexiglas box that was open at both ends. This box was then placed in a larger tank that was divided into two chambers by a partition with a hole through it. The membrane sealed around the fish's jaws was attached to the edge of the hole and sealed in place with a Plexiglas plate held with stainless steel wing nuts. This system allowed separation of the inspired and expired water, yet allowed the fish to make normal respiratory movements. Water level in the two chambers was maintained by standpipes (constant level drains). Ventilation volume was determined by measuring the water flow rate from the standpipe in the chamber containing the fish. By lowering this standpipe, the fish could be force-ventilated.

Water samples were drawn from the anterior chamber, and from the black Plexiglas box containing the fish, approximately every 15 to 20 min. Water oxygen level was determined with a water-jacketed oxygen electrode (Radiometer, Copenhagen) maintained at 25°C. Metabolic rate was calculated using the oxygen content difference between inspired and expired water and the ventilation volume.

Aholehole were given 2 h to recover from the anesthesia before metabolic rate measurements were begun. A series of metabolic rate measurements were made with the water level in the two chambers even and the fish actively pumping water over its gills, until the its metabolic rate remained relatively stable for at least 1 h. The water level in the chamber containing the fish was then lowered and measurements taken while the animal was being force-ventilated, continuing again until the metabolic rate stablized. Finally, the fish was given 0.1-0.3 mL Flaxedil (intramuscularly) and metabolic rate measurements continued while the animal was paralyzed and force-ventilated. In two cases, the fish was left in the respirometer overnight on forced ventilation to allow the effects of Flaxedil to wear off. Metabolic rate measurements were made again

before and after Flaxedil injection the next day. The SMR was calculated as the mean of the last four to six metabolic rate measurements. Water temperature was maintained at 25°C (±0.3) throughout the experiment.

The SMR of rainbow trout was directly determined in the same respirometry box as that used for tunas, using essentially identical methodology, except freshwater was used, inspired and expired water were sampled, and oxygen levels were measured with a water-jacketed Radiometer oxygen electrode.

RESULTS

Effects of Body Size on SMR

The SMR's of 21 kawakawa (0.540-2.153 kg) and 13 yellowfin tuna (0.585-3.890 kg) were determined at 25°C. Regression lines of SMR versus body weight were fitted by Gauss-Newton iteration (Biomedical Computer Programs, Program BMDP 3R), rather than a log-log transformation of the data (Fig. 1). The advantages of the former and disadvantages of the latter method are discussed by Zar (1968) and Glass (1969).

The best fitting allometric equations are

1) Kawakawa:
$$\text{SMR} = 392.5\ (\pm 32.3)\ W^{0.496\ (\pm 0.145)}$$
$$n = 21$$
2) Yellowfin tuna:
$$\text{SMR} = 286.8\ (\pm 26.9)\ W^{0.573\ (\pm 0.116)}$$
$$n = 13.$$

For comparison, the allometric equation relating

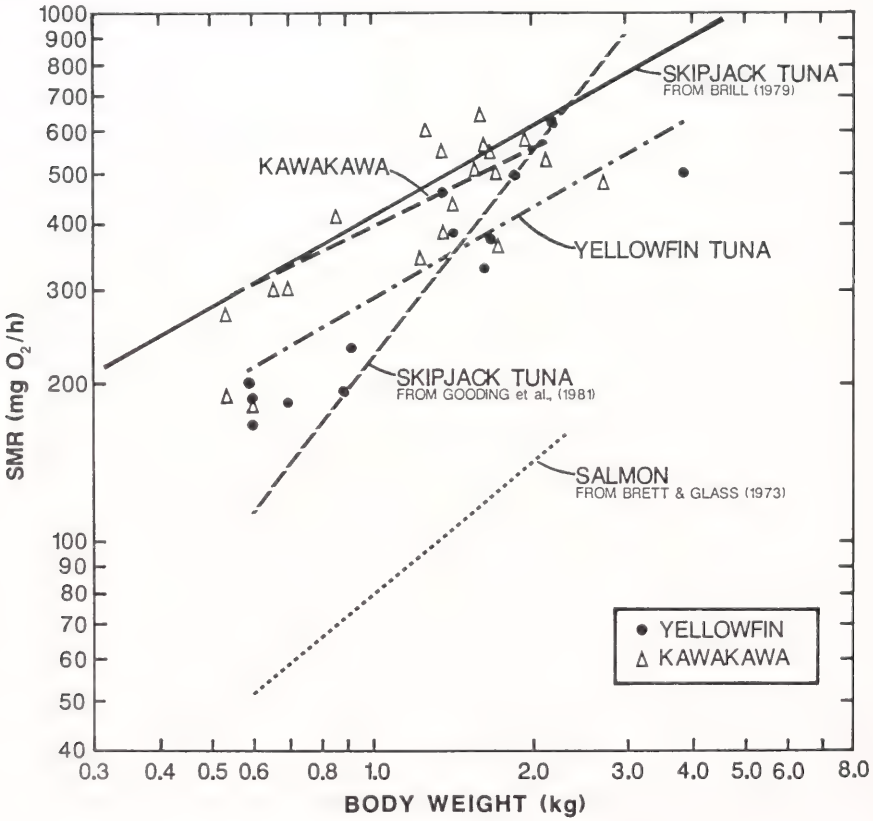

FIGURE 1.—A double logarithmic plot of the standard metabolic rates (SMR) of 13 yellowfin tuna and 21 kawakawa. The lines represent the allometric equations: SMR = 286.8 $W^{0.573}$, SMR = 392.5 $W^{0.496}$, and SMR = 412.0 $W^{0.563}$ for yellowfin tuna, kawakawa, and skipjack tuna, respectively, where the SMR is mg O_2/h and W is body weight in kilograms. The line for skipjack tuna is from Brill (1979). For comparison, the regression lines based on swimming skipjack tuna (Gooding et al. 1981) and for salmon at 20°C (Brett and Glass 1973) are also shown. All tuna data is from fish at 23°-25°C.

SMR and body weight in skipjack tuna is (Brill 1979)

$$SMR = 412.0\ (\pm 27.1)\ W^{0.563\ (\pm 0.07)}$$
$$n = 33.$$

The SMR is in mg O_2/h and W is body weight in kilograms. The values in parentheses are the standard errors of the parameters.

Effects of Acute Temperature Change on SMR, Heart Rate, and Excess Red Muscle Temperature

A total of 8 kawakawa, 12 yellowfin tuna, and 5 skipjack tuna were subjected to 5°C temperature changes. Most temperature changes were made between 20°C and 25°C, which all fish survived. Ten fish were exposed to 25° and 30°C, but only four survived long enough at 30°C to provide usable data. Because of the expense and difficulty in obtaining live tunas, the latter treatment was not pursued.

The SMR's and mean heart rates at 20°, 25°, and 30°C are given in Table 1. The Q_{10}'s of SMR for water temperatures changes from 20° to 25°C were variable and ranged from 5.82 to 1.39. The mean Q_{10}'s (±95% confidence intervals) were 2.44 ± 0.97, 2.31 ± 0.51, and 3.16 ± 0.93 for skipjack tuna, yellowfin tuna, and kawakawa, respectively.

The range of mean excess red muscle temperatures are given in Table 2. These excess muscle temperatures are lower than those measured in free swimming yellowfin and skipjack tunas (Dizon and Brill 1979). This is as expected because in paralyzed tunas, most of the heat production (i.e., energy consumption) most likely occurs at the heart and gills where the heat would not be retained by the vascular countercurrent heat exchangers.

The SMR of Aholehole and Rainbow Trout

Aholehole, unlike rainbow trout, will not sit quietly in a darkened respirometer box nor stop breathing movements when force-ventilated. Because Flaxedil

TABLE 1.—Effect of temperature on the standard metabolic rate and heart rate of yellowfin tuna, kawakawa, and skipjack tuna.

Species / Weight	SMR (mg O_2 h) 20°C	25°C	30°C	Q_{10} 20°-25°C	25°-30°C	Heart rate (min^{-1}) 20°C	25°C	30°C	Q_{10} 20°-25°C	25°-30°C
Yellowfin tuna										
2.215	470 ± 47	625 ± 53	—	1.77	—	89 ± 1	133 ± 2	—	2.21	—
1.438	258 ± 8	386 ± 21	605 ± 13	2.24	2.46	98 ± 1	146 ± 2	176 ± 1	2.22	1.45
1.635	161 ± 17	330 ± 17	—	4.20	—	81 ± 2	138 ± 2	—	2.89	—
3.890	311 ± 12	501 ± 32	—	2.60	—	57 ± 2	90 ± 2	—	2.49	—
0.704	112 ± 6	184 ± 6	—	2.70	—	99 ± 4	149 ± 1	—	2.26	—
0.877	150 ± 6	193 ± 6	—	1.66	—	77 ± 1	121 ± 3	—	2.45	—
0.599	103 ± 3	166 ± 6	—	2.60	—	73 ± 6	138 ± 8	—	3.55	—
0.595	153 ± 6	187 ± 6	—	1.49	—	74 ± 6	137 ± 5	—	3.41	—
0.585	154 ± 9	199 ± 3	266 ± 10	1.67	1.73	118 ± 1	159 ± 3	200 ± 2	1.82	1.58
1.290	333 ± 4	493 ± 17	—	2.19	—	106 ± 1	160 ± 2	—	2.28	—
Mean:				2.31	2.10				2.56	1.59
Standard deviation:				0.80	0.52				0.56	0.09
Kawakawa										
1.439	258 ± 12	431 ± 19	—	2.79	—	128 ± 1	205 ± 8	—	2.57	—
1.713	331 ± 12	497 ± 11	—	2.25	—	147 ± 2	213 ± 2	—	2.10	—
0.870	170 ± 14	410 ± 27	—	5.82	—	147 ± 4	217 ± 6	—	2.18	—
1.283	379 ± 9	598 ± 25	—	2.49	—	146 ± 14	206 ± 23	—	1.99	—
1.623	363 ± 27	640 ± 23	—	3.11	—	118 ± 4	175 ± 3	—	2.20	—
1.377	—	543 ± 35	761 ± 23	—	1.96	—	200 ± 14	272 ± 27	—	1.85
1.653	309 ± 7	560 ± 34	—	3.28	—	155 ± 1	221 ± 4	—	2.03	—
0.700	195 ± 10	300 ± 11	—	2.37	—	183 ± 4	253 ± 15	—	1.91	—
Mean:				3.16	1.96				2.14	1.85
Standard deviation:				1.23	—				0.22	—
Skipjack tuna										
1.069	140 ± 7	263 ± 22	—	3.53	—	78 ± 28	202 ± 4	—	6.71	—
0.582	214 ± 8	282 ± 6	386 ± 7	1.87	1.87	148 ± 2	237 ± 9	275 ± 20	2.56	1.35
0.425	173 ± 6	226 ± 11	—	1.71	—	122 ± 6	191 ± 5	—	2.45	—
0.448	179 ± 9	211 ± 8	—	1.39	—	134 ± 8	197 ± 3	—	2.16	—
0.629	113 ± 6	217 ± 7	—	3.71	—	145 ± 3	212 ± 3	—	2.14	—
Mean:				2.44	1.87				3.74	1.35
Standard error:				1.09	—				2.11	—

TABLE 2.—Range of mean (±SD) excess muscle temperatures in paralyzed tuna.

Tuna	20°C Mean	20°C SD	25°C Mean	25°C SD	30°C Mean	30°C SD
Kawakawa	0.7(±0.2)-1.9(±0.3)		0.5(±0.2)-1.5(±0.3)		[1]1.0(0.1)	
Yellowfin	0.3(±0.2)-1.4(±0.1)		0.0(±0.1)-0.7(±0.2)		0.2(±0.1)-0.4(±0.1)	
Skipjack	0.2(±0.1)-0.6(±0.1)		0.0(±0.2)-1.0(±0.2)		[1]0.6(±0.2)	

[1]Only one fish survived long enough to provide useful data.

stops all movements, all fish showed a decrease in metabolic rate after injection. The decrease ranged from 10 to 52% (mean 36%).

The directly measured SMR's from four aholehole and four rainbow trout paralyzed with Flaxedil are given in Table 3.

DISCUSSION

Adequacy of Directly Measured SMR

Muir et al. (1965) provided a regression equation for SMR versus weight for aholehole adapted to 23°C freshwater, based on extrapolation of swimming speed-metabolic rate curves back to zero swimming speed. The predicted freshwater SMR's based on their regression equation was increased by 75% to account for the higher osmoregulatory costs of seawater adapted animals (Nordlie and Leffler 1975). No correction was made for temperature. As shown in Table 3, in all cases but one, the directly measured SMR's are close to the SMR's based Muir et al.'s data when corrected for seawater adapted animals. With respect to rainbow trout, in all cases but one, directly measured SMR's are within one standard deviation of the SMR's obtained by extrapolation to zero swimming speed for rainbow trout at 15°C obtained by Bushnell et al. (1984). Therefore, directly measuring SMR's in Flaxedil-paralyzed aholehole and rainbow trout yields data that are similar to data obtained by the more widely used method of determining SMR by extrapolation of a swimming speed-metabolic rate curve back to zero swimming speed.

Tropical tuna species such as yellowfin, skipjack, and kawakawa will survive in a swimming tunnel for only short periods of time. Although other methods to control swimming speed (such as weighting and fin clipping, Dizon and Brill 1979; Boggs 1984) have been tried, they have met with only limited success. Therefore, direct measurement of SMR's using Flaxedil-paralyzed animals is for now the only way to obtain these data for tropical tuna species. As the data from aholehole and rainbow trout show, direct measure of SMR's using paralyzed animals yields results similar to that obtained by the more commonly used method of extrapolating swimming speed-metabolic rate curves back to zero swimming speed.

The heart rates (+1 SE, at 25°C) observed in this study were 230+20, 206+36, 132+17/min for skipjack tuna, kawakawa, and yellowfin tuna, respectively. These heart rates are higher than those observed for lightly anesthetized skipjack tuna (Stevens 1972), and are 60 and 39% higher than heart rates measured in skipjack and yellowfin tunas (respectively) that have been immobilized by spinal blockade with lidocaine and are force ventilated (unpubl. obs.). The heart rates measured in Flaxedil-paralyzed animals are, however, within the range exhibited by free-swimming skipjack tuna (80-240 beats/min, Kanwisher et al. 1974). The higher heart

TABLE 3.—Standard metabolic rate of aholehole and rainbow trout.

Oxygen consumption (mg O_2 kg^{-1} h^{-1}) ± SD					
Aholehole			Rainbow trout		
Weight (g)	Measured SMR	Predicted SMR[1]	Weight (g)	Measured SMR	Predicted SMR[2]
65.5	264(±12.2)	118	289	53.3(±3.8)	82.5±(27.4)
80.9	146(±16)	113	401	78.8(±7.0)	82.5±(27.4)
91.2	[3]135/127(±9.9/8.8)	111	403	60.5(±10.9)	82.5±(27.4)
108.5	[3]114/162(±11.1/12.0)	106	568	55.5(±9.9)	82.5±(27.4)

[1]Based on Muir et al. (1965) and corrected for saltwater adapted fish based on Nordlie and Leffler (1975).

[2]From Bushnell et al. (1984), for 250-350 g fish adapted to 15°C. No corrections for the weight dependence of SMR were provided.

[3]SMR determinations made approximately 20 h apart.

rates observed in paralyzed tunas may be due to the vagolytic action of Flaxedil (Grollman and Grollman 1970). However, as the data from aholehole and rainbow trout show, estimating SMR using animals paralyzed with Flaxedil and by extrapolation of swimming speed-metabolic rate curves back to zero swimming speed yield similar results.

Effect of Body Size and Acute Temperature Change on SMR

In Figure 1, it appears that the SMR's of yellowfin tuna are lower than those of skipjack tuna and kawakawa. However, based on the 95% confidence intervals, the heights of the regression lines (at mean body weights) are not significantly different from each other. Based on the 95% confidence intervals, the weight exponents of the regression equations for kawakawa, yellowfin tuna, and skipjack tuna also are not significantly different over the size ranges tested (Fig. 1). In other words, the effect of body weight on the SMR is not significantly different among the three tuna species. The exponent in the allometric equation describing the effect of body size on the SMR of other teleosts ranges from approximately 0.65 to >1 (Winberg 1956; Fry 1957; Beamish 1964; Beamish and Mookherjii 1964; Glass 1969; Brett 1972). The lower values of the exponents for tunas indicate that the weight specific SMR[5] (i.e., mg O_2/(g·h)) of tunas decreases more rapidly as body size increases than it does for other teleosts.

Gooding et al. (1981) also estimated the SMR of skipjack tuna. When converted to the same units used in this study (SMR in mg O_2/h and W in kg), the relationship they found for the effect of body weight on SMR was

$$\text{SMR} = 234\ W^{1.19}.$$

The exponent greater than one means that they predict the weight specific SMR to increase with increasing body size. As shown in Figure 1, Gooding et al.'s predicted SMR's are lower than mine for small fish, but exceed my estimates above approximately 2.5 kg body weight because of the large weight exponent.

To estimate SMR, Gooding et al. (1981) used a multiple linear regression equation of the logarithm of metabolic rate versus swimming speed and the logarithm of body weight, and then extrapolated back to zero swimming speed. Their data and extrapolations were based on several groups of different-sized fish swimming at voluntary speeds in a tank respirometer. This methodology is not equivalent to the more conventional one of estimating SMR based on swimming speed-metabolic rate curves that are constructed by forcing one fish, swimming in a tunnel respirometer, to undergo stepwise increases in swimming speed during which the fish remains for at least 1 h at each speed (Brett 1972). Furthermore, Gooding et al. (1981) expressed swimming speeds in body lengths per second. Boggs (1984) has shown that this will cause appreciable bias when fitting multiple linear regression equations because the effect of the body size on active metabolic rate is different at different swimming speeds.

The Effect of Acute Temperature Change on SMR and Heart Rate

As shown in Table 1, the Q_{10}'s (effect of temperature) for the SMR's of skipjack tuna, yellowfin tuna, and kawakawa are the same. They are also close to the Q_{10}'s for SMR's of other teleost species subjected to acute temperature change (Q_{10} = 2.16, Moffitt and Crawshaw 1983; Q_{10} = 2.10, Boehlert 1978), and for the effect of temperature on SMR where fish were acclimated to each test temperature (Q_{10} = 2.48, Ott et al. 1980; Q_{10} = 1.82-2.83, Duthie 1982).

This result was not expected since studies on the effect of temperature change on the metabolic rate of isolated red and white muscle samples (Gordon 1968, 1972a, 1972b), volitional swimming speed (Dizon et al. 1978), and preliminary work on active metabolic rate of skipjack tuna showed all three to be unaffected by temperature.

Comparing the metabolic rate (1,052 mg O_2/h, from Gooding et al. 1981) of a 2.0 kg skipjack tuna at its minimum swimming speed (1.4 body lengths/s) to its directly measured SMR (608 mg O_2/h, from Brill 1979), shows that the SMR constitutes 58% of the minimum swimming metabolic rate. Because skipjack tuna's SMR constitutes a large fraction of their metabolic rate at minimum swimming speeds and increases as temperature increases, whereas swimming metabolic rate and volitional swimming speed do not, increases in muscle efficiency (i.e., increases in thrust developed by the caudal propeller per unit of O_2 uptake), reductions in hydrodynamic drag (perhaps due to reduction in water viscosity), or unknown physiological adjustments must occur

[5]If the allometric equation to describe the effect of body size on whole body standard metabolic rate (SMR) is SMR = aW^b, then the corresponding equation to describe weight-specific SMR versus body weight is SMR/W = aW^b/W or SMR′ = aW^{b-1}; where SMR′ = weight-specific SMR, W = body weight, and a and b are fitted parameters.

when ambient temperature increases to keep active metabolic rate temperature independent.

The effect of water temperature (20°-25°C) on heart rate was variable (Q_{10}'s ranged from 6.71 to 1.82). The mean values (±95% confidence intervals) of 3.74 (±1.9), 2.56 (±0.35), 2.14 (±0.17) for skipjack tuna, yellowfin tuna, and kawakawa, respectively, are not significantly different from each other and are close to the Q_{10} (2-3) found for the effect of temperature on the heart rate of lingcod, *Ophiodon elongatus*, (Stevens et al. 1972).

Why Are The SMR's of Tunas So High?

Also shown in Figure 1 is the SMR-body weight relationship for sockeye salmon at 20°C, taken from Brett and Glass (1973). Even with the differences in the slopes of the lines, it is still apparent that tunas have remarkably high SMR's. In the following paragraphs, I argue (as did Stevens and Neill 1978; Stevens and Dizon 1982) that tunas are "energy speculators", gambling high rates of energy expenditure against high rates of energy return. I also hypothesize that tunas' physiology and anatomy have evolved to increase maximum sustainable (i.e., aerobic) metabolic rates (MMR's) and that high SMR's are an inevitable consequence of this ability. In other words, high SMR's are a result of anatomical and physiological adaptations (primarily large gill surface areas) associated with high MMR's. Tunas have high MMR's and high SMR's, whereas sluggish bottom-dwelling flatfish (e.g., *Platichthys fleusus*) have low MMR's and low SMR's (Duthie 1982). Active fish like salmon have MMR's and SMR's intermediate between these two extremes (Brett 1972).

Advantages of High Maximum Metabolic Rates

Tunas live in the open ocean, an environment which provides no shelter and where patches of forage are widely scattered (Sund et al. 1981). In this environment, high sustainable swimming speeds (i.e., high MMR's) enable tunas to travel quickly between food patches and to search large volumes of water in the least amount of time. Also, tunas have been shown to have very high rates of digestion (Magnuson 1969), which is advantageous for species that must be able to fully exploit a food patch whenever one is found. Since digestion is an energy consuming process, high rates of oxygen delivery and blood flow are required for high rates of digestion.

Because the pelagic environment provides tuna no place to hide and rest while repaying an oxygen debt, the ability to quickly metabolize lactate is also advantageous. High MMR's therefore allow tuna to rapidly repay an oxygen debt when one is accumulated. Tuna's only defense against predators such as blue marlin, *Makaira nigricans*, is presumably a burst of maximum (i.e., anaerobic) swimming. Prey capture by tunas also must involve some high speed swimming. Coulson (1979) has argued that the ability to achieve high rates of anaerobic glycolysis allows vertebrate ectotherms to successfully compete with vertebrate endotherms, which are capable of much higher rates of aerobic metabolism. However, most vertebrate ectotherms, whether terrestrial or aquatic, must spend long quiescent periods to metabolize lactate (Coulson et al. 1977). Yet tunas have the ability to metabolize some of the highest muscle lactate levels ever recorded in vertebrates in only a few hours (Barrett and Connor 1964; Hochachka et al. 1978). Other teleosts may take as long as 24 h to recover from severe exercise even though they accumulate lower white muscle lactate concentrations (Black et al. 1961; Wardle 1978). Tunas' vascular heat exchangers appear to also aid the rapid movement of lactate from the white muscle where it is produced to the red muscle where it is presumably metabolized (Stevens and Carey 1981).

Although using different terminology, McNab (1980) citing terrestrial vertebrates and Pauly (1981) citing fishes, both argue that given certain constraints, high MMR's are advantageous because rates of somatic and gonadal growth are dependent upon rates of delivery of oxygen and substrate to the tissues. Indeed, Pauly (1981) has shown that the growth rates of fishes are proportional to, and perhaps controlled by, gill surface area. Furthermore, he suggests that it is maximum rate of oxygen delivery to the tissues, rather than food supply, that limits growth rates and that species like tunas, which have the largest gill surface areas, have the highest growth rates. Koch and Wieser (1983) have shown that fish reduce activity levels during periods of gonadal growth. Tunas cannot make this trade off. For tunas, it is probably necessary to maintain a high rate of activity during gonadal synthesis which, in turn, requires respiratory and cardiovascular systems capable of delivering oxygen and metabolic substrates to the tissues at high rates.

Adaptations of Tunas For Achieving High Maximum Metabolic Rates

In a series of studies on the MMR's in land mammals (see Taylor and Weibel 1981, and the papers

that follow), pulmonary diffusing capacity, mitochondrial volume and capillary density in muscles were shown to be limiting factors in achieving high MMR's. From these studies Weibel et al. (1981) proposed that, at maximum rates of aerobic metabolism, there is no excess capacity at any level in the respiratory chain. In other words, to achieve high MMR's, a complete series of anatomical/physiological/biochemical adaptations must be present. And, as shown in Table 4, these adaptations are present in tunas.

TABLE 4.—Adaptations of tunas for high maximum metabolic rates.

Large gill surface areas	Muir and Hughes 1969
Thin secondary lamella in the gills	Muir and Brown 1971
High hematocrit, high hemoglobin levels (i.e., high blood O_2 carrying capacity)	Klawe et al. 1963; Jones et al. 1986
High maximum cardiac output	Poupa and Lindstrom 1983
Elevated muscle temperatures	Stevens and Neill 1978 Stevens 1982
High muscle myoglobin levels	George and Stevens 1978 Stevens and Carey 1981
High muscle mitochondrial density	George and Stevens 1978 Hulbert et al. 1979
High muscle capillary density	Hulbert et al. 1979
High muscle aerobic enzyme activity levels	Guppy et al. 1979

One of tunas' adaptations for high MMR's are gills with large respiratory surface areas. However, high rates of oxygen uptake are inexorably linked with high osmoregulatory costs, since gills that permit high rates of oxygen uptake must also permit high rates of water and ion movements. This is especially true in marine fishes like tunas where seawater and blood osmolality are approximately 1,000 and 400 mosm, respectively (Bourke 1983). Rao (1968), Farmer and Beamish (1969), Nordlie and Leffler (1975), and Furspan et al. (1984) estimated that the cost of osmoregulation can account for 27 to 50% of the SMR. The gills are a main osmoregulatory effector organ (Evans 1979), and Daxboeck et al. (1982) found that gill tissue respiration alone can account for 27% of the SMR in trout. The SMR, therefore, is obviously strongly influenced by osmoregulatory cost, which in turn is strongly influenced by gill surface area. Ultsch (1973, 1976) came to a similar conclusion after finding that the SMR's of aquatic (i.e., gill breathing) salamanders were controlled by respiratory (i.e., gill) surface area.

Muir and Hughes (1969) measured the total secondary lamellar gill surface (i.e., respiratory) area in skipjack tuna, yellowfin tuna, and bluefin tuna, *Thunnus thunnus*. They found total secondary lamellar areas for 1 kg tunas to be an order of magnitude or more larger than 1 kg bass or roach. Also, they found gill areas were proportional to body weight and the exponent to be 0.85 for the combined data from the three tuna species. This exponent is significantly different from the exponents I found for the effect of body weight on SMR's. It appears that in tunas, the SMR is not strictly determined by secondary lamellar surface area, although high osmoregulatory costs are most likely the main cause of tunas' high SMR's. Also, the difference between the effct of body size on SMR and gill respiratory area implies that larger tunas have greater scope of activity than smaller fishes, as has been shown to occur in other teleosts (Hughes 1984).

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VARIATIONS IN THE BLOOD CHEMISTRY OF THE LOGGERHEAD SEA TURTLE, *CARETTA CARETTA*

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ABSTRACT

The natural blood chemistry profile of loggerhead sea turtles living in Cape Canaveral waters was determined over a 3-year period. Overall plasma osmotic pressure, potassium, and magnesium values were similar to those reported for other reptiles, sodium and chloride was much less than for sea snakes. Plasma calcium and glucose values were among the lowest of any reptile. Osmotic pressure, sodium, and potassium values increased during the warmer months. Chloride and in particular magnesium, glucose, and hematocrit levels were comparatively constant. Calcium and urea values showed wide variations but no seasonal trend was apparent. Changes in urea concentrations closely tracked those of osmotic pressure. Blood lactate values from trawl-captured sea turtles were 10-80 times higher than those from quiescent sea turtles and calculations suggest that at least 20 hours is required for full recovery. The complex changes in blood chemistry observed reflect changes in the sea turtle physiology and biochemistry; significant changes from normal in plasma magnesium, potassium, and hematocrit could be useful indicators of hibernation in sea turtles.

For any animal a knowledge of the normal pattern and changes in blood chemistry can be related to its physiological state and can also be used to identify chronic and pathological conditions. With the exception of sea turtles, there are many studies and reviews on seasonal changes in the blood chemistry of reptiles (Dessauer 1970; Duguy 1970; Gilles-Baillien 1974; Minnich 1982). Since there is an urgent need to understand the ecological physiology of these endangered and threatened species, this lack of information on sea turtles is undoubtedly due to the logistical difficulties of long-term sampling of a wild marine population.

The year-round presence of large numbers of loggerhead sea turtles, *Caretta caretta*, in and around the Port Canaveral ship channel provided a rare opportunity to study the monthly changes that occur in the biology of this little understood group of animals. Such a study was rendered all the more urgent by finding, in the winter of 1978, numerous black stained and apparently torpid turtles lodged in the mud of the ship channel (Carr et al. 1980). It was suggested that the loggerhead sea turtle was able to survive prolonged exposure to cold seawater temperatures (less than 15°C) by partially lodging in the mud at the bottom of the Port Canaveral ship channel and by going into a state of winter dormancy or apparent hibernation (Carr et al. 1980; Ogren and McVea 1982). If this hypothesis were correct, it would mean that the Cape Canaveral ship channel was serving as a hibernaculum for this endangered species and the identification of features that could confirm hibernation in these loggerhead sea turtles was of some practical importance. For this purpose, a study of blood chemistry is particularly apt. There is abundant evidence of significant changes in certain blood constituents in hibernating mammals (Fisher and Manery 1967; Soivio and Kristoffersson 1974; Al-Badry and Taha 1983) and there are a few studies showing similar changes in some reptiles (e.g., freshwater turtles, Hutton and Goodnight 1957; lizards, Haggag et al. 1965).

The purpose of this study was to establish the normal seasonal changes in blood chemistry that occur throughout the year in the Cape Canaveral population of loggerhead sea turtles and from this base of data to identify, if found, those animals that are in a state of hibernation.

METHODS

Selected National Marine Fisheries Service (NMFS) shrimp trawl turtle surveys of the Port Canaveral ship channel were accompanied by the authors from December 1978 to August 1982. On board ship the activity levels of newly caught loggerhead sea turtles were observed, and body temperature, weight, and sex recorded. Blood samples were taken from freshly captured sea turtles, using a heparinised syringe, from a venous sinus on the

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lateral dorsal region of the neck (Bentley and Dunbar-Cooper 1980). Some sea turtles were also resampled after 3, 4, and 5 h on deck. The hematocrit was measured on board ship immediately after taking the sample. Blood cells were centrifuged and plasma stored on ice for transport to Miami. The plasma was frozen until used (−4°C).

The items that were measured are as follows: Plasma osmotic pressure, using a Wescor vapor pressure osmometer; sodium and potassium concentrations, by flame emission spectrophotometry; calcium and magnesium, by atomic absorption spectrophotometry using appropriate standards (Lutz 1972); chloride, using an Aminco Chloridometer; and urea and glucose, using enzymatic kit techniques (Sigma).

The blood chemistry values reported are means ± SD. Statistical differences between groups were determined with Student's t test, and level of significance was set at $P < 0.05$ for all comparisons.

RESULTS

Hematocrit

The hematocrit levels of the loggerhead sea turtle were remarkably constant and were not influenced by season (Table 1). The range of values was 28-48%, and the mean 35.4% is very similar to that found by Dessauer (1970) for the same species (32%). The sea turtles caught in December 1978 were a striking exception to this uniformity with very much lower mean hematocrits (15%) and one individual having a value as low as 5%.

Loggerhead sea turtles resampled 3-5 h after capture showed some interesting changes. Four animals resampled after 3 h on deck showed an average increase in hematocrit of 10.4% (±14.89), for five animals after 4 h the average increase was 4.8% (±4.7), and for four animals after 5 h the hematocrit had decreased on average 15.2 (±13.3) from the initial value. The reason for this change is not clear.

TABLE 1.—Blood chemistry values of loggerhead sea turtles trapped by shrimp trawl in the Port Canaveral of samples in parentheses. Groups that differ significantly

Date	°C	Na	K	Ca	Mg	Cl
Dec. 1979	21.0	150.2 ± 13.45 (5)	3.7 ± 0.81 (4)	1.09 ± 0.50 (5)	*1.7 ± 0.46 (5)	109.3 ± 11.36 (4)
Jan. 1980	18.0	138.1 ± 13.07 (11)	3.3 ± 0.49 (11)	1.4 ± 0.48 (13)	2.19 ± 0.30 (13)	105.9 ± 8.40 (11)
Feb. 1980	16.0	129.2 ± 12.7 (8)	3.05 ± 0.63 (8)	1.18 ± 0.86 (8)	1.84 ± 0.46 (8)	110.5 ± 11.71 (8)
Mar. 1980	18.0	142.2 ± 8.95 (6)	3.32 ± 0.63 (6)	1.04 ± 0.38 (7)	2.2 ± 0.56 (7)	108.6 ± 4.36 (5)
Apr. 1980	19.0	140.9 ± 4.7 (4)	3.58 ± 0.37 (4)	1.03 ± 0.16 (4)	2.24 ± 0.42 (4)	112 ± 10.42 (4)
May 1980	23.0	139.3	3.5	—	—	112
June 1980	24.0	139.5 ± 5.87 (6)	3.5 ± 0.40 (6)	0.86 ± 0.50 (5)	2.29 ± 0.41 (5)	103.5 ± 9.02 (5)
July 1980	25.0	143.1 ± 5.55 (7)	3.9 ± 0.83 (7)	1.08 ± 0.77 (7)	2.38 ± 0.39 (7)	*114.4 ± 3.34 (7)
Aug. 1980	28.0	139.5	—	1.58	1.75	121
Sept. 1980	—	145.2 ± 10.95 (5)	3.8 ± 0.65 (5)	1.4 ± 0.3 (5)	2.23 ± 0.46 (5)	**121.8 ± 16.4 (7)
Nov. 1981	24.0	**162.2 ± 7.93 (5)	**4.18 ± 1.49 (5)	**2.18 ± 0.325 (9)	1.49 ± 0.77 (5)	107.0 ± 3.25 (9)
Feb. 1982	19.0	142.07 ± 21.42 (4)	4.145 ± 0.69 (4)	1.863 ± 0.456 (5)	1.976 ± 0.303 (5)	102.7 ± 10.58 (10)
Mar. 1982	18.0	152.1 ± 14.2 (5)	**4.17 ± 0.454 (5)	1.40 ± 0.765 (10)	2.31 ± 0.66 (5)	108.86 ± 9.88 (10)
May 1982	24.5	*165.5 ± 4.41 (3)	*4.08 ± 2.04 (3)	2.09 ± 0.41 (8)	2.00 ± 0.62 (4)	110.3 ± 5.62 (9)
June 1982	27.0	**168.9 ± 4.09 (3)	**4.6 ± 0.48 (3)	1.78 ± 0.93 (10)	1.93 ± 0.55 (5)	108.2 ± 13.0 (9)
Aug. 1982	—	*159.3 ± 15.4 (5)	5.14 ± 0.83 (5)	1.69 ± 0.96 (8)	2.65 ± 0.69 (5)	**117.3 ± 6.57 (9)

It is too short a time lapse for an erythropoesis response particularly as sea turtle red cells can have life spans of 600-800 d (Altman and Brace 1962); but it is possible that the loggerhead sea turtle has a considerable ability to store and release blood cells on demand.

Sodium

Plasma sodium increased as the year advanced with minimal values found in February of each year followed by a gradual rise to maximums in late summer and early fall (Table 1). However, the range of values is very wide (Table 1); the lowest for an individual was 105.5 m*M*, the highest 173.0 m*M*. The mean sodium concentration for the whole population was 145.03 ± 13.80 m*M* (n = 82).

Chloride

Like sodium the highest values were found in the fall (Table 1), but the individual range, 102.7-131.2 m*M*, was much narrower than that found for sodium. The narrow excursion suggests that chloride is under comparatively tight control. The population average, 107.2 ± 18.80 m*M* (n = 86) is very similar to that reported by Dessauer (1970) (110 m*M*).

Potassium

The field data showed little change in the absolute potassium levels (Table 1). The population mean 3.82 ± 0.764 m*M* (n = 70) is considerably lower than that found for salt water adapted Malaclemys (8.8 m*M*, Dunson 1970). Minimal values were found in early spring (February) and a gradual rise was seen as summer advanced.

Calcium

Calcium values ranged quite widely over the sampling period and the results are fairly scattered and

ship channel, December 1979 - August 1982. Unless otherwise stated, units are m*M*. Mean ± SD, number from January 1980 group (* $P < 0.05$; ** $P < 0.01$).

Date	°C	Lactate	Glucose	Urea	Osmotic pressure mOsm	Hematocrit %
Dec. 1979	21.0	—	—	10.9 ± 6.64 (5)	315.2 ± 15.2 (5)	**15.67 ± 8.10 (4)
Jan. 1980	18.0	—	—	6.19 ± 2.82 (11)	301.5 ± 22.6 (11)	34.9 ± 2.70 (9)
Feb. 1980	16.0	—	—	4.56 ± 1.86 (8)	300.4 ± 20.6 (7)	36.1 ± 7.18 (7)
Mar. 1980	18.0	—	—	5.02 ± 1.44 (5)	*324.8 ± 9.06 (6)	35.0 ± 5.19 (8)
Apr. 1980	19.0	—	—	**15.5 ± 9.72 (4)	340.5 ± 16.09 (4)	37.8 ± 7.63 (4)
May 1980	23.0	—	—	9.22	334	35.3 ± 5.90 (4)
June 1980	24.0	—	—	2.28 ± 2.46 (6)	305.3 ± 19.1 (6)	34.3 ± 4.35 (9)
July 1980	25.0	—	—	5.73 ± 6.66 (7)	*329.4 ± 26.27 (7)	35.5 ± 6.87 (6)
Aug. 1980	28.0	—	—	6.8	327	32.9 ± 4.8 (2)
Sept. 1980	—	—	—	7.8 ± 2.61 (5)	*332.6 ± 9.81 (5)	34.3 ± 4.89 (7)
Nov. 1981	24.0	—	—	9.43 ± 4.56 (9)	*330.1 ± 19.12 (9)	35.3 ± 5.27 (9)
Feb. 1982	19.0	3.51 ± 0.27 (4)	1.17 ± 0.367 (4)	6.78 ± 2.04 (10)	309.0 ± 28.8 (10)	33.7 ± 5.85 (10)
Mar. 1982	18.0	3.42 ± 1.39 (4)	0.98 ± 0.468 (3)	5.55 ± 2.51 (10)	309 ± 9.36 (10)	36.1 ± 5.71 (10)
May 1982	27.0	3.58 ± 0.07 (3)	1.31	4.41 ± 3.8 (10)	*329.4 ± 20.3 (10)	31.8 ± 3.60
June 1982	24.5	—	—	4.45 ± 2.11 (9)	314.8 ± 10.9 (9)	34.08 ± 5.46 (6)
Aug. 1982	—	**16.2 ± 8.1 (3)	1.12 ± 0.18 (3)	6.19 ± 4.49 (9)	*343.3 ± 23.1 (9)	33.0 ± 2.68 (7)

no pattern is discernable, peaks being found in November and May (Table 1). The lowest plasma calcium for an individual was 0.19 m*M* and the highest 4.90 m*M*. For the whole population the mean is 1.53 ± 0.76 m*M* (n = 115).

Magnesium

The population mean is 2.10 ± 0.542 m*M* (n = 88). The lowest and highest values for individuals were 0.96 and 3.80 m*M* respectively, a smaller excursion than that found for calcium. It appears that plasma magnesium levels are under comparatively tight control.

Osmotic Pressure

The osmotic pressure values showed the greatest absolute excursion, individuals ranging from 258 to 360 mOsm. The lowest monthly means were found from January to March of each year (Table 1). The average osmotic pressure for the whole population was 321.3 ± 24.10 mOsm (n = 117).

Urea

Plama urea values showed the greatest relative range in individuals, 0.4-23.8 m*M*. Interestingly, the pattern of changes is remarkably similar to that of the osmotic pressure (Fig. 1), suggesting strongly that both are linked in some way. The mean value for the population (6.57 ± 5.82 m*M*, n = 101) is very similar to that reported for the same species (6.0 m*M*, Dessauer 1970).

Glucose

In the field blood glucose was remarkably steady at about 1 m*M* (Table 1), suggesting that blood glucose levels are highly regulated. This value is considerably lower than that reported earlier for the loggerhead sea turtle (3.3 m*M*, Dessauer 1970).

Lactate

For most loggerhead sea turtles the blood lactate concentrations ranged from 3 to 4 m*M* shortly after capture (Table 1). However, noticeably higher lactate values (8.8-16.2 m*M*) were obtained from sea turtles caught in a single trawl (August 1982). This was possibly the result of more severe trawl stress. Rates of recovery while on deck varied. For 6 individuals, lactate had declined an average of 16.8% from the initial value after 3 h; for 4 sea turtles after 4 h, average lactate had declined 52.6%; and for 4 sea turtles lactate had declined 16.4% after 5 h.

DISCUSSION

This study examines, for the first time, the monthly changes in the blood chemistry of a marine turtle. However it must be borne in mind that this is a field study without "controls" and alterations in body chemistry and metabolism could be due to intrinsic biological rhythms cued to extrinsic factors such as photoperiod or could be directly determined by environmental changes in, for example, temperature. As turtles are ectotherms (with the possible exception of leatherbacks) seasonal changes in temperature will be accompanied by matching changes in body temperature. It was not possible, therefore, to distinguish between temperature effects per se and changes due to annual rhythms acting as Zeitgebers. Temperature effects are the subject of a separate study (Lutz and Dunbar-Cooper 1984).

The total sample number assembled over the course of this study for each blood constituent is very large, as far as we are aware the set is much

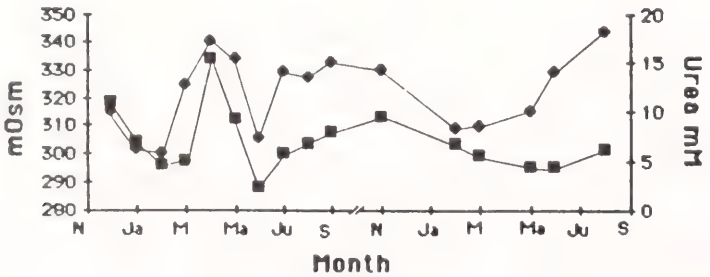

FIGURE 1.—Seasonal changes in plasma urea (■) and osmotic pressure (♦) in the loggerhead sea turtle, December 1979 to September 1981 and November 1981 to August 1982.

larger than any previous study on reptiles, and allows some general comments on the composition of sea turtle blood to be made.

The osmotic pressure found in this study, of 321 mOsm, is significantly lower than that found by Schoffeniels and Tercafs (1965) for the loggerhead sea turtle (465 mOsm), and the value 408 mOsm quoted by Dessauer (1970). It is, however, similar to that found for other reptiles including crocodiles and freshwater turtles (about 290 mOsm, Dessauer 1970). The observation, therefore, that marine turtles have relatively high osmotic pressures (Minnich 1982) would appear unwarranted. Plasma sodium and chloride concentrations are so much less than those reported for the sea snake *Pelamis platus* caught in the wild (Na = 210 m*M*, Cl = 167 m*M*, Dunson and Elhart 1971) that phylogenetic considerations may be involved. Potassium values found in this study (3.8 m*M*) fall within the range characteristic of other reptiles (3-6 m*M*, Dessauer 1970) arguing against the observation that sea turtles have peculiarly high potassium concentrations (Dessauer 1970). Magnesium values are similar to those reported for other turtles, including sea turtles (Minnich 1982) but calcium is rather low (1.5 m*M* this study, 3.1 m*M* quoted by Dessauer 1970). As mentioned above, the hematocrit, glucose, and urea data agree with earlier estimations.

The changes observed in this study are of considerably physiological significance if internal ionic concentrations are used to regulate the activity of ion sensitive metabolic pathways (Lutz 1975) particularly if some salts, such as Na, K, and Cl, have highly perturbing effects on enzyme function (Hochachka and Somero 1984).

The contrast between the behaviour of sodium and chloride is of interest. Sodium shows a wide excursion in values throughout the year with several peaks and troughs but tends to rise as the year progresses. Compared with sodium, chloride is relatively constant and the minor changes that do occur do not match in time with those of sodium. Although both ions account for most of the plasma osmotic pressure (78.5%), neither by themselves was significantly related to osmotic pressure. Changes in either sodium or chloride do not determine changes in osmotic pressure. Lance (1976) found likewise that plasma sodium showed a much wider excursion than plasma chloride in the cobra *Naja naja*, but in this species only a single summer sodium peak was seen. It is noteworthy that the lowest sodium values were found in the coldest month (February 1980, Table 1). A winter decrease in plasma sodium has been found for several freshwater turtle species, particularly those hibernating (Gilles-Baillien 1974).

We found that plasma potassium increased as the summer progressed and laboratory data suggests that this may be a temperature related phenomenon (Lutz and Dunbar-Cooper 1984). A rise in plasma potassium during the warmer months has also been observed in the lizard *Trachysaurus rugosus* and the terrapin *Malaclemys centreta* (Gilles-Baillien 1973). However, the pattern is not constant; a fall has been seen in *Varanus grisus* (Haggag et al. 1965) and no change seen in *Pseudemys scripta* (Hutton and Goodnight 1957).

Although highly variable, calcium values are low. There are several peaks per year but no consistent pattern was seen. It is very likely, however, that the changes in blood calcium reflect changes in physiology. High values have been found in some reptiles during vitellogenesis (as high as 34 m*M*, Lance 1976) and calcium has also been found to rise to extraordinary high levels in cold torpoid freshwater turtles (Jackson et al. 1984).

The seasonal changes in magnesium were much smaller over this study suggesting that wide excursions from this narrow range would be indicative of exceptional circumstances.

One of the most remarkable findings of this study is the parallel sweeps in the patterns shown by blood urea and osmotic pressure. As far as we are aware such a phenomenon has not been reported before. It is not simply a matter of changes in urea concentrations causing changes of osmotic pressure since the magnitude of the urea changes are much less than those of osmotic pressure. An integrated response is called for; possibly the perturbing effects of increasing osmotic pressure are compensated by heightened urea levels (Yancey et al. 1982). In loggerhead sea turtles, blood urea concentration would not appear to be diet determined since we observed that captured loggerhead sea turtles held at RSMAS, which were all fed the same food, had widely different urea values (range 3-21 m*M*). Interestingly, the field group with outstandingly high urea levels (April 1980) were all males.

The unchanging glucose levels demonstrate a high degree of conservatism. Seasonal changes in blood glucose have been observed in alligators with higher levels in the summer (Coulson and Hernandez 1980). In *P. scripta*, on the other hand, blood glucose increases during winter (Hutton and Goodnight 1957).

The hematocrit was also remarkable in its constancy, contrasting with other reptiles where seasonal changes in hematocrit have been recorded; typically as an increase during winter (Duguy 1970; Gilles-Baillien 1974). In contrast, the very low values

for December 1978 stand out strongly as a set by themselves and indicate some special condition.

The lactate values are of interest in that they give an index of the stress of capture in the trawl net. For quiescent loggerhead sea turtles kept in captivity at RSMAS, blood lactate is very low (0.2-0.4 m*M*). The initial blood lactate values obtained on deck were, by contrast, 10-80 times higher (3.2-16.2 m*M*, Table 1). Down to at least 3-4 m*M*, the rate of lactate recovery for sea turtles held on board was clearly concentration dependent (Fig. 2, $P < 0.01$). If the rate did not further decline, then it would take about 20 h for full recovery of the least stressed sea turtles in this study (those with initial blood lactate values of 3-4 m*M*). If the rate of decline continued to be concentration dependent then the recovery time would be much greater.

Unfortunately, since no lethargic loggerhead sea turtles were found during this study, one of its principle objectives, the identification of the state of hibernation in sea turtle, was not realizable. This occurred because South Florida has been blessed with warm winters since 1975 and water temperatures have not been lower than 15°C in the Cape Canaveral region. Nevertheless, the wealth of information on the seasonal changes in blood chemistry we now have is sufficient to enable a clear diagnosis of hibernation in sea turtles if and when animals in this condition are found. Magnesium is a prime candidate for such a purpose, since this study identifies the normal range for plasma magnesium throughout the year. Substantial increases in blood magnesium have been seen in many hibernating animals, including mammals and reptiles (Haggag et al. 1965; Soivio and Kristoffersson 1974; Al-Badry et al. 1983). Significant changes in plasma sodium and potassium have also been associated with hibernation in reptiles (Gilles-Baillien 1974). The normal range of potassium is so narrow that extraordinarily high values should be easily detected. Substantial increases in blood lactate have been associated with cold torpor in several freshwater turtles (Jackson et al. 1984); however, as we have seen elevated blood lactate can occur with stress. And finally hematocrit is of high interest since significant changes in hematocrit, both increases and decreases, have been widely reported in hibernating reptiles (Gilles-Baillien 1974). With a single exception, hematocrit was remarkably steady over the course of this survey, and perhaps significantly, the exception occurred in the coldest month encountered. Perhaps the very low hematocrits found in December 1979 were part of a preparatory condition for hibernation.

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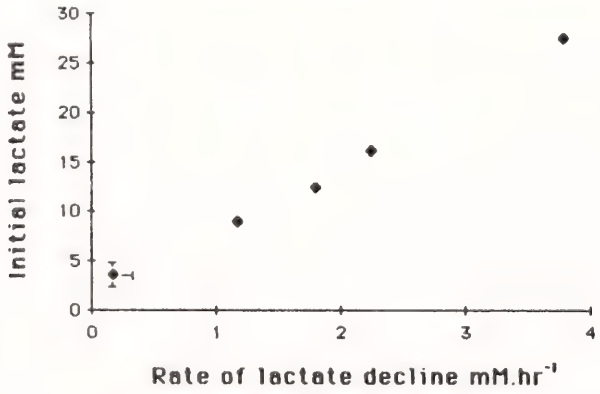

Figure 2.—Rate of blood lactate decline compared to initial lactate concentration for shrimp trawl trapped loggerhead sea turtles held on board ship for 3-5 h. For the lowest data point $n = 11$, SDs are illustrated. For other data points $n = 1$.

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EFFECTS OF AIR EXPOSURE ON DESICCATION RATE, HEMOLYMPH CHEMISTRY, AND ESCAPE BEHAVIOR OF THE SPINY LOBSTER, *PANULIRUS ARGUS*

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ABSTRACT

Desiccation rates and hemolymph pH, lactic acid and ammonia concentrations of spiny lobsters, *Panulirus argus*, exposed in air for up to 2 hours were measured. Desiccation rates were faster in smaller lobsters. During a 2-hour exposure, hemolymph lactic acid levels increased more than 11 times, pH decreased more than one-half unit, and ammonia concentrations nearly doubled. Exposure-induced changes in hemolymph parameters occurred most rapidly in the first 30 minutes and began to level off by 2 hours. Lobsters exposed for 2 hours, then reimmersed for 24 hours, survived and had normal hemolymph chemical values. However, 75% of the reimmersed spiny lobsters had a delayed or absent tail-flip escape response; most individuals also exhibited diminished antennal defensive motions. Results suggest that desiccation and hemolymph chemical changes, caused by exposure, do not directly cause mortality, but rather induce secondary physiological damage, manifested as aberrant defensive and escape behavior.

The South Florida fishery for spiny lobster, *Panulirus argus* (Latreille, 1804), uses sublegal (<76 mm carapace length, CL) lobsters, locally called shorts, as living attractants in traps for legal-sized lobsters. Shorts used in this manner are customarily held in wooden boxes on deck until replaced in traps. Aerial exposure ranges from a few minutes to several hours but is typically about 1 h (Bill Moore[2]). Hunt et al. (1986) reported an average 26.3% mortality rate after 4 wk for lobsters that had been exposed between ½ and 4 h and estimated that 600,000 to 3.7 million shorts die annually as a result of handling and exposure. Because this mortality is incurred by sublegal lobsters which otherwise would soon contribute to legal harvest, economic loss to the fishery is considerable, perhaps as high as $9.0 million annually.

This study examines desiccation rate, hemolymph chemistry, and escape behavior of spiny lobster to document physiological and behavioral changes induced by air exposure. The relationship between these changes and mortality is discussed.

MATERIALS AND METHODS

One hundred seventy intermolt spiny lobsters, averaging 80.2 mm CL (range, 56.7-120.7 mm), were collected from traps at the Atlantic reefs south of Marathon, FL, in the Florida Keys. Approximately 26 lobsters at one time were allowed to acclimate for a minimum of 2 d in a 800 L (179 × 76 × 60 cm) outdoor fiberglass tank. The tank was fully shaded by three plywood sections which could be removed individually, allowing easy access while minimizing disturbance. Flow-through water circulation was maintained by a pump drawing approximately 3,600 L/hour from a clean, well-oxygenated canal. Complete water exchange occurred every 15 min. Periodic canal water samples had oxygen concentrations of 5-7 ppm and no detectable ammonia or lactic acid. There were resident spiny lobsters in the canal.

Shelter inside the tank was provided by a double layer of two-hole cinder blocks (39.5 × 19.5 × 19.5 cm) centered and aligned parallel to the long axis of the tank. This arrangement of blocks allowed for easy removal of spiny lobsters by the antenna-tug technique, described later. In rare instances when a spiny lobster evaded capture on the first attempt, sampling of that animal was postponed for at least 24 h. This was necessary because repeated tail-flips depressed hemolymph pH (unpubl. data). Spiny lobsters were not fed during confinement or held longer than 10 d. Both sexes were used equally.

Desiccation Rate

Spiny lobsters were randomly selected from the acclimation tank at 10 min intervals, marked for in-

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dividual identification, and alternately assigned to either an exposure or control group.

After marking, control spiny lobsters were weighed to the nearest 0.1 g and promptly placed inside a shaded, wood-slat fish box two-thirds submerged inside the acclimation tank. Weights were also recorded at 1 and 2 h. Excess water clinging to the exoskeleton and inside the branchial chambers was removed prior to each weighing by holding the spiny lobster around the carapace in a head down position and gently moving it through a short downward arc six times. Exposed spiny lobsters were marked and weighed as above, but were held in a fish box located in a fully shaded outdoor area. Evaporative water loss was indicated by weight decrease over time.

During the period when desiccation experiments were performed (late March to early May 1984), relative humidity was 61-72%, air temperature 22-30°C, wind speed 10 km/h or less, and cloud cover ranged from clear to lightly scattered or hazy. Experiments were not performed on very wet or windy days to avoid excessive variation in desiccation rates between experiments.

Hemolymph Chemistry

To assess effects of exposure on hemolymph chemistry, spiny lobsters were air-exposed in fish boxes for ½, 1, or 2 h as previously described. Control spiny lobsters were removed directly from the acclimation tank.

Hemolymph sampling was via cardiac puncture. A 1.6 mm (1/16-in) hole drilled through the dorsal carapace directly over the heart allowed easy hypodermic removal of 8-10 mL of hemolymph. There is no suitable chemical method to prevent hemolymph clotting (Young 1972). At ambient temperature, spiny lobster hemolymph forms a tough rubbery clot within seconds. Prompt cooling of the hemolymph by immersion of the syringe in an ice water bath (4°C, 60 s) inhibited clotting long enough to prepare subsamples for pH, ammonia, and lactic acid analysis. All hemolymph samples were collected between the hours of 10:00 and 16:00 and analyzed the same day.

Intervals between netting and completion of hemolymph removal were 70 s or less, thus minimizing trauma associated with handling and cardiac puncture. Since net confinement reduced struggling, spiny lobsters were not removed from the net for hemolymph sampling unless access to the dorsal carapace was restricted. In preliminary experiments, repetitive handling and sampling of controls depressed hemolymph pH values. Consequently, each spiny lobster was sampled only once in experiments reported here. Hemolymph pH was determined by a digital pH meter with a calomel microelectrode. Hemolymph subsamples (2 mL) and a 7.0 buffer solution were chilled to 4°C in a second ice water bath before recording pH. Blood pH at 4°C probably varies from in vivo pH at ambient temperature, but this was an essential concession to retard clot formation. Anaerobic, radiometer-type pH measurements were also impossible due to clotting. However, care was taken to minimize hemolymph air contact since changes in CO_2 equilibrium can alter pH values. Truchot (1975) reported the pH of crustacean blood exposed to air without mixing varies little from anaerobically obtained samples.

Serum was prepared by injecting the remaining 6-8 mL of chilled hemolymph into a 15 mL tissue grinder, then gently grinding for 1-2 min until the clotting hemolymph was liquified. The still cool serum was then refrigerated in capped test tubes for subsequent ammonia analysis.

Ammonia was measured using the Conway microdiffusion method (Conway and Byrne 1933) with modifications suggested by Seligson and Seligson (1951). With this method, ammonia from a 0.5 mL blood sample was diffused onto an acidified glass rod inserted inside a microdiffusion cell. Microdiffusion cells were rotated for 50 min to facilitate diffusion, then the rods were washed off with 5 mL of Nessler's reagent. Intensity of color developed in Nessler's reagent, corresponding to ammonia concentration, was measured in a colorimeter at 420 nm. All samples were done in duplicate as were blanks and two concentration standards (10 μg/mL and 20 μg/mL) accompanying each group of unknowns.

Blood serum lactic acid concentrations were determined with a Sigma Chemical Company[3] lactic acid analysis kit (826UV). With this kit, blood lactic acid is converted to pyruvic acid by lactate dehydrogenase, resulting in reduction of an equivalent amount of NAD. Reduction of NAD causes an increase in sample absorbance at 340 nm proportional to the initial lactic acid concentration. The same 2 mL blood sample used to measure pH was subsequently deproteinated with 4 mL of 8% perchloric acid and used in the lactic acid analysis. After 90-min incubation of the reaction mixture at 25°C, absorbance readings were stable, indicating the end point of the reaction. A chemical modification of the

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Sigma kit hydrazine buffer, recommended by Graham et al. (1983) for cases of end point instability, was not used because stable end points were obtained after 90 min.

One group of spiny lobsters was exposed for 2 h and then returned to the acclimation tank for 24 h before sampling to observe whether the blood chemistry changes which I observed immediately after exposure persisted after reimmersion.

Escape Behavior

Controls were individually netted, marked, and returned to the tank in less than 1 min. Exposed spiny lobsters were netted, marked, and placed in a shaded fish box for 2 h before being returned to the tank. Twenty-four h later, spiny lobsters were netted from the tank again and escape responses were recorded. A delayed or absent tail-flip after an antenna touch or tug was considered an impaired escape response; an immediate tail-flip was considered normal.

Student's t-test was used to analyze all desiccation and hemolymph chemical data. Values of $P < 0.05$ were considered significant. All data are expressed as means ± 1 SE. Since the control hemolymph chemical values from each exposure interval and from the reimmersed exposed spiny lobster experiment were not significantly different, they were pooled.

RESULTS

Desiccation Rate

Control spiny lobsters, which remained submerged except during weighings, maintained constant weights (Table 1). Percentage of initial weight remaining at the end of 2-h air exposure was 95.30% for shorts and 96.37% for legals, or an average weight loss of 2.35%/hour and 1.82%/hour respectively.

Hemolymph Chemistry

During a 2-h exposure, hemolymph lactic acid levels increased more than 11 times (from 4.4 mg/100 mL to 49.5 mg/100 mL), pH decreased more than one-half unit (from 7.91 to 7.40), and ammonia concentration nearly doubled (from 7.22 μg/mL to 13.77 μg/mL) (Fig. 1). Exposure-induced changes in hemolymph parameters occurred very rapidly then leveled off. Lactic acid and pH changed more in the first 30 min of exposure than in the subsequent 90 min. Ammonia accumulation was also at its maximum rate during the first 30 min.

All spiny lobsters exposed for 2 h, then returned to the acclimation tank for 24 h before sampling, survived and had normal hemolymph parameters (Fig. 1). Evidently, acute hemolymph effects of exposure (i.e., elevated lactic acid and ammonia, depressed pH) do not persist beyond 24 h.

Escape Behavior

Nonexposed spiny lobsters defended their positions in the concrete block holes with vigorous antennal movements directed toward an approaching hand until contact was made. Then a tap or, more frequently, a light tug on the tip of one antenna elicited an immediate tail-flip, propelling the lobster backward into the net. This method of removing lobsters from the acclimation tank was 100% effective on nonexposed lobsters.

Although hemolymph parameters of exposed spiny lobsters returned to normal within 24 h after reimmersion, it was evident that defensive and escape behavior of these lobsters was abnormal. In lobsters exposed for 2 h and then reimmersed for 24 h, defensive antennal movements were feeble or absent, and an antennal tap or tug usually failed to elicit an immediate escape response. When it did occur, the tail-flip response required several strong antennal tugs over a 3-4 s period. In some cases, a tail-flip could not be induced by any form of anten-

TABLE 1.—Percentage of initial spiny lobster weight remaining after various exposure times. Data are means ± 1 SE; N is in parentheses. Differences between shorts and legals are significant at 2 h but not 1 h.

	Exposure time (hours)					
	0	N	1	N	2	N
Controls	100.00	(15)	100.21 ± 0.09	(15)	100.15 ± 0.14	(15)
Shorts	100.00	(14)	97.60 ± 0.13	(13)	95.30 ± 0.18	(14)
Legals	100.00	(9)	97.68 ± 0.17	(8)	96.37 ± 0.27	(9)
Shorts and legals combined	100.00	(23)	97.70 ± 0.11	(21)	95.72 ± 0.19	(23)

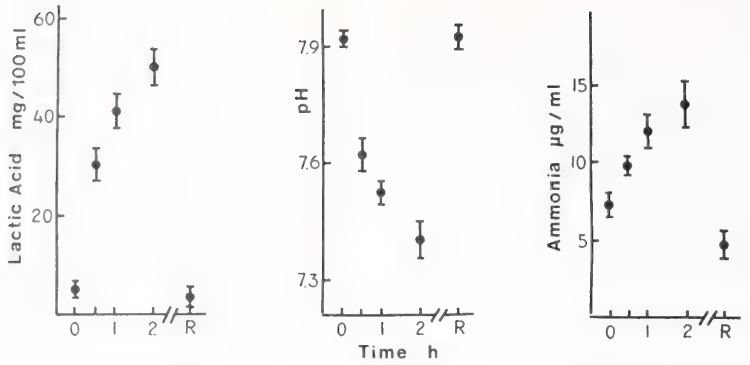

FIGURE 1.—Hemolymph lactic acid, pH and ammonia concentrations of spiny lobsters after air exposures of 0 (controls, pooled values), ½, 1, and 2 h. R = chemical values after 2-h exposure followed by 24-h reimmersion. N = 45, 20, 17, 16, and 20 for 0, ½, 1, 2, and R, respectively.

nal manipulation. The degree of antennal defensive movements was difficult to quantify, so the observation of feeble or absent movements is given here as anecdotal information. None of the immersed (control) lobsters showed an impaired tail-flip, whereas 75% of previously exposed lobsters showed some tail-flip impairment, i.e., tail-flip delayed or absent (Table 2). Controls tested again after 24 h still showed no tail-flip impairment, indicating that observed behavioral aberrations were not caused by netting and were not learned net-avoidance behavior.

TABLE 2.—Escape response (E.R.) impairment 24 h after 2-h exposure. Lobsters with delayed or absent tail-flip response to an antenna tug were considered impaired.

	Time (h)	Total no. netted	Normal E.R.	Impaired E.R.	Impaired (%)
Controls	0	15	15	0	0
	24	15	15	0	0
Exposed	0	20	20	0	0
(First run)	24	20	5	15	75
Exposed	0	12	12	0	0
(Second run)	24	12	3	9	75

DISCUSSION

Aquatic organisms suffer water loss and other stresses during air exposure. Inability to ventilate gills may lead to hypoxia, anaerobic metabolism, and accumulation of toxic metabolites. Intertidal crustaceans, which are periodically exposed to air, have behavioral, anatomical, and physiological adaptations that moderate deleterious effects of exposure. The barnacle, *Pollicipes polymerus*, easily recovers after a 40-50% water loss (Fyhn et al. 1972). Barnacles can reduce their metabolic rate during emersion and tolerate extended periods of anaerobiosis (Barnes et al. 1963). The stone crab, *Menippe mercenaria*, can survive severe hypoxia for at least 12 h at 28°-30°C and can tolerate high levels of hemolymph lactate (Albert and Ellington 1985). Crustaceans that have made a permanent transition from water to land have even more elaborate adaptations to the special rigors of the terrestrial environment (Bliss 1968). Terrestrial decapods (e.g., *Cardisoma* and *Gecarcinus*) exhibit extensive anatomical modifications of the gills and branchial chambers, including a reduction in gill number, volume, and area, which presumably minimize desiccation effects, and strongly sclerotized and ridged gills which do not collapse in air (Pearse 1950; Gray 1957; Edney 1960). Enhanced exoskeletal resistance to water loss is also a common adaptation of semiterrestrial and terrestrial crustacean species. Aquatic decapods in air lose 3-5 times as much water as do terrestrial decapods (Herreid 1969).

The spiny lobster lives subtidally throughout its life cycle and is only exposed to air as a byproduct of present fishery practices. Because there has been no selective pressure to evolve behavioral, anatomical, or physiological adaptations to aerial exposure, tolerance by spiny lobster should be low. Present results support that contention. Exposing spiny lobsters for even relatively short periods results in metabolic acidosis, accumulation of the toxic excretory product, ammonia, and impairment of defensive and escape behavior after reimmersion.

Desiccation Rate

Desiccation rate results are only valid for the range of weather conditions previously specified. Higher temperature and wind speed increases desiccation rate whereas higher relative humidity decreases it.

Because rate of water loss is directly proportional to surface area, smaller spiny lobsters, with higher surface area to volume ratios, lose water at a faster rate. If desiccation is indeed a major stress factor, smaller (sublegal) spiny lobsters will be more affected.

This size-desiccation rate relationship has also been noted by other investigators. Lazo-Wasem (1984) reported that smaller terrestrial amphipods, *Arcitalitrus sylvaticus*, lost water faster than did larger amphipods; he suggested a higher surface area to volume ratio and higher respiratory rate of smaller amphipods as two possible explanations. Davies (1969) reported that rate of water loss in a limpet, *Patella* sp., varied inversely with body weight. Price (1980) reported similar results in an intertidal snail, *Melampus bidentatus*.

Spiny lobsters exposed for 2 h lost only 3.6-4.7% of their initial weight, so it is unlikely that simple dehydration is a major source of exposure stress. This conclusion is supported by experiments showing that periodic wetting of spiny lobster with seawater during exposure did not improve survival (Hunt et al. 1986). McLeese (1965) also reported that continuous sprays of seawater did not increase survival of air-exposed northern lobsters, *Homarus americanus*. It has been suggested that gill damage caused by dehydration may contribute to documented mortality in exposed western rock lobsters, *Panulirus cygnus* (Anonymous 1980), but this has not been demonstrated.

Hemolymph Chemistry

Subtidal crustaceans are unable to extract oxygen effectively from air. In *Cancer productus*, gas exchange rate is reduced fivefold in air (deFur and McMahon 1978). The European lobster, *Homarus vulgaris*, only extracts one-seventh as much oxygen from air as from water (Thomas 1954). It has not been reported how much aerial respiration *P. argus* can achieve, but the rapid transition to anaerobic metabolism during exposure indicates oxygen extraction from air is not adequate to support normal aerobic metabolism. Although gill bailers continue their paddle-like motions in air, loss of fluid support for gill filaments causes them to collapse (pers. obs.). Loss of gill surface area for gaseous exchange, coupled with a probable reduction in gill bailer efficiency in air, leads to the hemolymph chemistry changes observed. Lactic acid, the primary product of crustacean anaerobic glycolysis (Albert and Ellington 1985) accumulates in quantities sufficient to overwhelm protein and bicarbonate-carbonic acid hemolymph buffering. Taylor and Wheatly (1980) reported a 0.44 unit drop in arterial pH for the crayfish, *Austropotamobius pallipes*, after 3 h of air exposure. They attributed this acidosis to a tenfold increase in hemolymph lactate and to accumulation of CO_2. Organisms generally regulate pH precisely, because a high or low pH can disrupt enzymatic reactions, ionic/osmoregulatory control, and cell membrane stability (Prosser 1973).

Jonas et al. (1962) found a close link between blood pH and mortality in trout. Death resulted when blood pH was lowered with either dilute lactic acid or hydrochloric acid from a normal mean pH of 7.3 to 6.8-6.9, a decrease of 0.4-0.5 units. Fatalities did not result when injection of the same quantity of either acid did not lower blood pH into this 6.8-6.9 range. This indicates that acidosis was the cause of death rather than the acids themselves. Spiny lobsters exposed for 2 h experienced a similar 0.5 unit drop in pH (7.91-7.40). Lobsters evidently have a higher tolerance for acidosis than do trout, since a 2-h exposure was not immediately lethal. However, a pH change this large must be considered a large physiological perturbation. Acidosis may also compound oxygen extraction problems, since hemocyanin oxygen affinity decreases as pH falls. Alternatively, because lactate increases hemocyanin oxygen affinity (Truchot 1980; Mangum 1983), these effects may offset each other.

Crustaceans do not have efficient systems for metabolizing lactate, so its removal from hemolymph is relatively protracted (Ellington 1983). Bridges and Brand (1980) subjected six species of crustaceans to 5-8 h of hypoxia and observed that intertidal and burrowing species returned to near normal hemolymph lactate levels much faster (4-6 h) than subtidal, nonburrowing species (20-24 h). They suggested that species more likely to encounter hypoxia in their natural environments are better adapted for removing accumulated lactate when aerobic conditions return. The spiny lobster, as a subtidal, nonburrowing species, probably removes lactate slowly even though normal concentrations were restored within 24 h.

Spiny lobsters are ammonotelic and eliminate ammonia by diffusion from the gills into the respiratory stream and out into the water. Removing spiny

lobsters from the water eliminates the respiratory stream and the normal excretory route for ammonia. This toxic product of protein catabolism can then accumulate in the hemolymph.

Binns (1969) reported 16 μg/mL of ammonia in blood of freshly captured shore crabs, *Carcinus maenas*. Spaargaren (1982) reported blood ammonia concentrations between 4 and 9 μg/mL for this same species and also provided evidence for a close connection between ammonia excretion and extracellular ion regulation. Florkin (1960) reported average blood ammonia concentrations for 12 aquatic decapods to be 13 μg/mL, range 4-25 μg/mL. Normal hemolymph ammonia concentrations (7.22 μg/mL) for spiny lobsters are toward the low end of this range. After 2-h exposure, hemolymph ammonia concentrations for spiny lobster increased to 13.77 μg/mL. It is not known if this concentration is toxic; however, hypoxia has been reported to increase toxic effects of ammonia in minnows (Wuhrmann 1952), rainbow trout (Downing and Merkens 1955), and mice (Warren and Schenker 1960). Exposure-induced hypoxia in the spiny lobster may interact synergistically with ammonia, leading to toxic effects at concentrations that would not normally cause problems.

Ionized ammonia (NH_4+) is less toxic than unionized ammonia (NH_3) because of its lower tissue permeability (Warren and Nathan 1958). A decrease in hemolymph pH, as occurs during exposure, would shift the chemical equilibrium toward the less toxic NH_4+ (Warren and Schenker 1962). Exposure-induced acidosis may afford some protection against ammonia toxicity by this mechanism if ammonia does indeed reach concentrations toxic to spiny lobsters. Ammonia, which functions as a base, may also partially offset the pH decrease caused by lactic acid.

Escape Behavior and Conclusions

All 32 spiny lobsters exposed for 2 h and then reimmersed were alive after 24 h and had normal hemolymph chemical values. Apparently the acute effects of exposure (acidosis, ammonia, and lactic acid accumulation) do not directly cause the increased mortality reported in previous studies (Lyons and Kennedy 1981; Hunt et al. 1986). Rather, secondary physiological damage, persisting after acute effects have vanished, may be the ultimate cause of mortality. Persistant physiological damage was manifested as aberrant defensive and escape behavior.

Spiny lobsters with diminished antennal defensive movements and tail-flip escape responses would be at increased risk from predators. Brown and Caputi (1983) observed that western rock lobsters, *Panulirus cygnus*, exposed to air for ½-2 h were generally less active, slower in seeking shelter, incapable of defense, and more subject to attack by finfish and octopus.

Exposure effects severe enough to disrupt a basic reflex such as the tail-flip may also affect integrated nervous system functions such as feeding, locomotion, and social and sexual behavior. Nervous tissue is particularly susceptible to damage from hypoxia (Prosser 1973) and from fluctuations in osmotic and/or ionic concentrations of body fluids (Treherne 1980). Nervous system damage induced by hypoxia, acidosis, and perhaps osmotic imbalances is likely the cause of behavioral aberrations in exposed spiny lobsters.

Because the transition to anaerobic metabolism and resulting hemolymph changes occur so rapidly after emersion, the threshold at which physiological effects appear may be no more than a few minutes exposure. Fishery practices which allow exposures of 1 h or more must therefore be producing large numbers of spiny lobsters that are physiologically and behaviorally impaired.

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JUVENILE BLUE CRAB, *CALLINECTES SAPIDUS*, SURVIVAL: AN EVALUATION OF EELGRASS, *ZOSTERA MARINA*, AS REFUGE

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ABSTRACT

Field experiments were conducted to examine rates of predation on juvenile blue crabs in different densities of eelgrass near Manahawkin, New Jersey. Tethering experiments from July to October 1985 showed that crabs in eelgrass were preyed on at lower rates than those in adjacent bare sand patches. In addition, intermediate densities of eelgrass provided the best refuge for blue crabs while crabs in low- and high-density eelgrass suffered higher rates of predation. We suggest that the root mats of high-density eelgrass may reduce the ability of blue crabs to hide and bury in the substratum. There was no effect of prey size (11-100 mm carapace width) on risk to predation. Predation on sand substrate declined during the observation period and rates dropped to zero in vegetation in October.

The blue crab, *Callinectes sapidus*, is one of the most important commercial species in mid-Atlantic coastal waters of the United States (Van Engel 1958; Williams 1984). Blue crabs are caught in abundance from Florida into New Jersey waters, and are taken in lesser numbers as far north as Nova Scotia (Williams 1984). Although the Chesapeake Bay system produces the greatest catches of blue crabs, commercial and recreational fishing is significant in many other Atlantic bays and estuaries.

Despite the economic importance of blue crabs and the large amount of prior research done on this species, there are many unanswered questions about the factors that influence blue crab abundance and distribution (Williams 1984), and our ability to predict annual harvests is extremely limited. The stages of the life cycle that are least understood are the larval and juvenile stages, and it is these which suffer most nonfishing mortality.

Studies of blue crab larval transport have shown that wind-driven circulation patterns influence the abundance of larvae that enter mid-Atlantic coast estuaries (Sulkin et al. 1980; Epifanio and Dittel 1982; McConnaugha et al. 1983; Provenzano et al. 1983; Epifanio et al. 1984; Johnson et al. 1984; Sulkin 1984). In addition, we know that juvenile blue crabs in most estuaries are found in much greater abundance in stands of submerged vegetation than on unvegetated substrate (Tagatz 1968; Diaz and Fredette 1982; Kennish et al. 1982; Penry 1982; Zimmerman and Minello 1984), and it is believed that submerged vegetation provides protection from predators for small blue crabs and for crabs undergoing ecdysis (Lippson 1973; Heck and Orth 1980; Heck and Thoman 1984; Orth et al. 1984). To date no studies have demonstrated that submerged vegetation actually provides protection for juvenile blue crabs under field conditions nor do we have data on the influence of vegetation density on survival of blue crabs. Below we describe the results of a series of field experiments designed to evaluate the protective properties of varying densities of eelgrass, *Zostera marina*, for different size classes of blue crabs. We also report on the identity of potential predators and estimate the role of submerged vegetation as it influences blue crab populations in New Jersey bays.

METHODS

Tethering experiments were conducted from July to October 1985 in shallow-water seagrass meadows near Manahawkin, NJ (lat. 39°N; long. 74°W). In this area, sand patches are interspersed among extensive seagrass beds dominated by *Zostera marina* (Macomber and Allen 1979). Large numbers of blue crabs inhabit these grass beds (cf. Kennish et al. 1984), just as they do in eelgrass beds of Chesapeake Bay (Heck and Orth 1980; Heck and Thoman 1984).

Blue crabs were collected by seine or dip net from *Zostera marina* and adjacent sand patches and prepared for tethering in the laboratory. No soft crabs

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(recently molted) were used in the experiments. Tethering of crabs was accomplished by tieing one end of a 1 m long piece of monofilament fishing line around the width of the body and securing the loop with "Super" glue (cyanoacrylate) to the top of the carapace. The other end of the line was tied to a J-shaped, heavy piece of wire (or stake) which was pushed into the sediment in the chosen seagrass or sand location. The super glue ensures that crabs do not escape and that a piece of the carapace is left on the line as evidence if predation does occur. The carapace width (CW) of all crabs was measured before placement in the field. For blue crabs larger than 40 mm CW, a 20-lb test steel leader was attached to the monofilament loop around the crab to prevent the cutting of the tether by the crabs' claws. Tethering techniques measure relative rates of predation and are used for comparison of mortality among sites. It is not intended to measure absolute rates of predation in any single habitat. Heck and Thoman (1981) provided an additional description of the tethering procedure.

A single blue crab was tethered to an individual stake, and three to four stakes were placed in each plant density and in unvegetated sand patches for each 24-h trial. The tethered crabs were left at the site for 24 h (+/−1 h), recovered, and predation losses scored. Twenty trials, utilizing a total of 218 crabs, were conducted from 15 July through 7 October.

The density of the seagrass was determined frequently during the study period by measuring dry weight biomass of the grass removed from 0.062 m^2 plots. Four samples with three replicates for each sample at each density were taken, and dry weights measured after drying at 100°C.

RESULTS

Vegetation clearly provides cover from predators for blue crabs (Fig. 1) as predation was always more intense in unvegetated sand patches than in seagrass. Relative rates of predation on tethered crabs on sand ranged from 24% to a high of 74% eaten per day. A 3-way contingency table analysis (survival × density × date) found significant interactions ($P < 0.01$) between crab survival and density of vegetation. Differences in predation rates among time periods were not statistically significant, although predation rates dropped steadily on sand after the middle of August and no predation was recorded in vegetation in October (Fig. 1). The influence of body size (CW) of crabs (Fig. 2) on risk to predation was also tested in a Kolmogorov-Smirnov test and found not significant ($P > 0.05$).

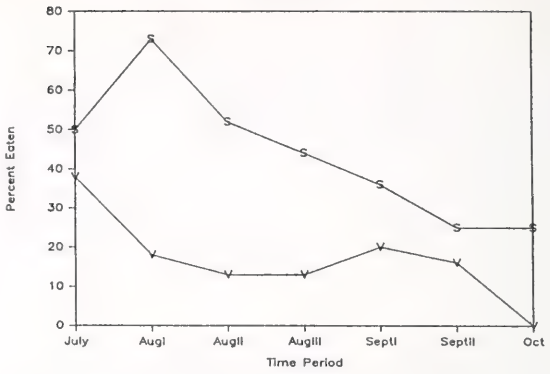

FIGURE 1.—Percent juvenile blue crabs eaten in sand (S) or vegetation (V), July to October 1985. Time period is broken into 2-3 wk periods.

Predation rate varied among densities of eelgrass (Fig. 3). Medium density seagrass provided the best refuge from predation with only 9% eaten per day ($N = 45$). A mean of over 19% per day was eaten in low-density ($N = 47$) and high-density ($N = 44$) grass sites. A Dunn's Multiple Comparison test (Hollander and Wolfe 1973) was used to analyze the predation-vegetation density data from July through September, excluding October because no predation occurred in eelgrass during that month. Predation rates in low and high densities were found to be significantly greater ($P < 0.05$) than in medium-density eelgrass.

Eelgrass biomass in low, medium, and high density 0.062 m^2 plots (Table 1) was found to be significantly different in a one-way analysis of variance ($P < 0.001$). Scheffé contrasts found that the mean dry weight of medium-density plots was significantly higher than low-density and significantly lower than high-density eelgrass plots.

TABLE 1.—Mean dry weights (g/0.062 m^2) of vegetation from experimental plots. **Significantly different at the $P < 0.01$ level.

Density	Mean	SD	P
Low	12.19	5.24	**
Medium	43.24	17.07	**
High	79.04	11.47	**

DISCUSSION

These data confirm results from other experimental studies of predation on decapod crustaceans (Heck and Thoman 1981; Orth and van Montfrans

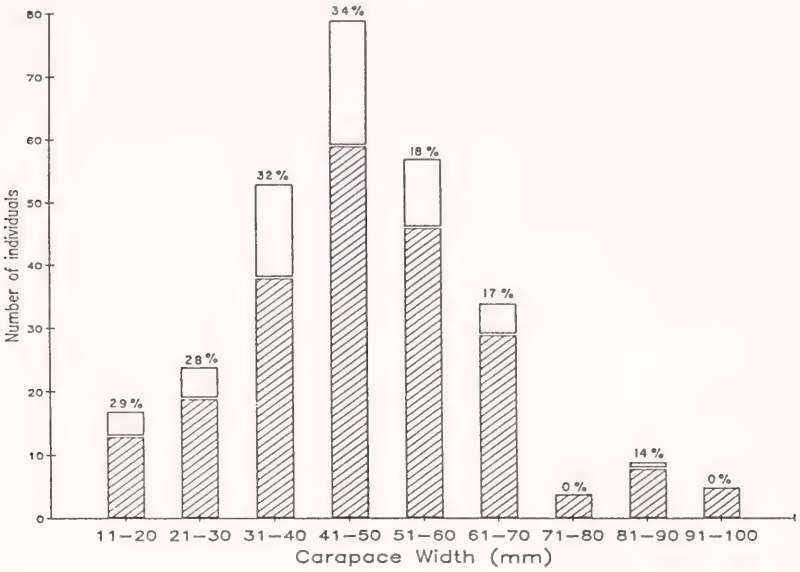

FIGURE 2.—Blue crab body size (carapace width (CW)) and risk of predation. Hatched bars indicate number of individuals tethered at that size and open bars indicate number of tethered crabs eaten.

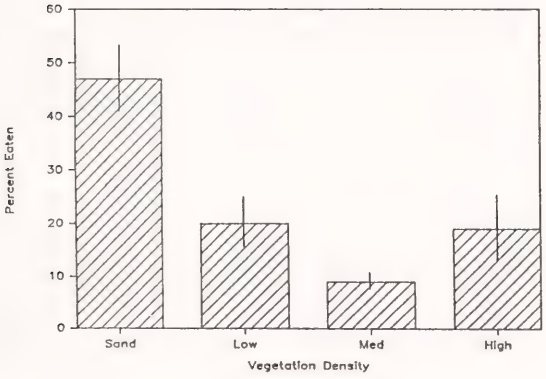

FIGURE 3.—The effect of eelgrass density on predation rates. Histograms are mean rates of predation from July through October on sand and at each eelgrass density. Vertical bars are +/− one standard error.

1982) and amphipods (Stoner 1982) that describe the importance of seagrasses as protective cover for prey. They clearly show that eelgrass provides refuge from predation and increased survival for juvenile blue crabs compared to that on adjacent unvegetated sand substrates.

Rates of predation on blue crabs within the three densities of vegetation, however, did not conform to patterns previously established, where predation on crustacean epifauna is inversely proportional to vegetation biomass (Stoner 1982; Leber 1985). In this study, risk of predation was lowest in intermediate densities rather than in high-density eelgrass.

Savino and Stein (1982) found that attack rates by largemouth bass on bluegills dramatically declined with increasing density of artificial vegetation, and capture rates by the predators were lower in vegetation than on bare substratum. Epifaunal amphipods and caridean shrimp also suffer lower rates of predation at high densities of vegetation (Nelson 1979; Stoner 1980; Coen et al. 1981; Leber 1985). These studies and others (Vince et al. 1976; Crowder and Cooper 1982; Minello and Zimmerman 1983) indicate that above-ground vegetation biomass reduces a visual predator's search and capture efficiencies and that vegetation may also provide a matching background in which epifaunal prey may hide (Endler 1978; Orth et al. 1984).

The root and rhizome mat of seagrasses may also lower search and capture efficiency of predators (Orth 1977; Blundon and Kennedy 1982b; Peterson 1982), but in addition a high-density root mat may reduce the ability of hard-bodied prey to bury and hide in the substratum. For example, Brenchley (1982) found that the burrowing ability of decapods in dense eelgrass root mats was reduced or prevented, and Bertness and Miller (1984) found that fiddler crabs, *Uca pugnax*, preferred to construct burrows in intermediate densities of salt marsh roots.

Juvenile blue crabs, unlike epifaunal caridean shrimp or amphipods, utilize below-ground refuges in seagrass beds. Our field and laboratory observations suggest that their primary mode of predator avoidance is to bury in the substratum. Orth and van Montfrans (1982) also noted burying behavior of juvenile blue crabs in laboratory experiments that examined predation by adult blue crabs in three densities of artificial seagrass and root mat. Their data also suggested mortality of juveniles is lowest in intermediate densities of seagrass.

We infer that at low seagrass densities the blue crabs are able to bury in the substratum, but the leaves and root mat of the grass do not reduce detection and capture efficiency of the predators as do intermediate seagrass densities. Furthermore, we suggest that the dense root mat and shoots of high-density seagrass may reduce the ability of blue crabs to bury themselves and that high blade density may reduce the crabs' visual ability to detect predators.

Based on our observations the dominant predators on blue crabs appear to be toadfish, *Opsanus tau*, the American eel, *Anguilla rostrata*, and other blue crabs. Toadfish are extremely common in the Manahawkin grass beds in the summer (June-September) and are known to readily consume brachyuran crabs, including blue crabs (Schwartz and Dutcher 1963; McDermott 1965; Wilson et al. 1982; Gibbons and Castagna 1985). In this study, there were instances where, upon recovery of tethers after a predation trial, toadfish had swallowed both the crab and tether and remained on the line, providing confirmation that toadfish are blue crab predators under field experimental conditions. Gut contents of American eels from the study area contained blue crabs (K. Able, pers. obs.) and Wenner and Musick (1975) found blue crabs to be a major part of the eel's diet.

Predation intensity appears to be distributed evenly over the size classes tested, although there is a trend of lower predation rates on the largest blue crabs (>71 mm CW). However, the sample size is small for these size classes (N = 17) so the estimate of predation on larger crabs may be inadequate. Escape in size has been observed in other invertebrate prey (Blundon and Kennedy 1982a; Peterson 1982; Wilson 1985) and a similar pattern was expected in this study because large adult blue crabs are found frequently on unvegetated substratum where risk of predation is highest (Heck and Thoman 1984). An additional large predator, the smooth dogfish, *Mustelus canis*, occurs in Barnegat Bay (Tatham et al. 1983) and we suspect it may feed on blue crabs in seagrass meadows at night (Casterlin and Reynolds 1979). *Mustelus* can grow to 1.5 m (Hildebrand and Schroeder 1928) and preys on blue crabs in eelgrass beds (Bigelow and Schroeder 1953). Hence, predation by smooth dogfish may account for loss of larger crabs and also suggests that there may be a temporal as well as spatial pattern of predation.

Researchers have suggested that the value of refuges for juvenile blue crabs and other invertebrate macrofauna is dependent on the interaction of several factors including species of vegetation, vegetation density, water quality, and type of predator (Heck and Thoman 1984; Orth et al. 1984). The data from these tethering experiments clearly indicate that eelgrass serves as protective cover and that eelgrass density is indeed an important factor in determining predation rates on juvenile blue crabs. The unexpected result that crabs in intermediate densities of eelgrass suffered lower predation rates than those in high densities underscores the complexity of the interactions that determine survival of juvenile blue crabs.

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FISH PREDATION ON JUVENILE BROWN SHRIMP, *PENAEUS AZTECUS* IVES: EFFECTS OF TURBIDITY AND SUBSTRATUM ON PREDATION RATES

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ABSTRACT

Predation on juvenile brown shrimp, *Penaeus aztecus*, by three species of estuarine fishes was examined in a series of laboratory experiments to determine the effect of turbid water and the presence of a suitable substratum for burrowing. Regardless of the type of substratum, turbid water increased predation by southern flounder, *Paralichthys lethostigma*, and decreased predation by Atlantic croaker, *Micropogonias undulatus*. In both clear and turbid water, the presence of sand, which allowed shrimp to burrow, decreased predation by southern flounder but had no significant effect on feeding rates of Atlantic croaker. There was a significant interaction between the effects of turbidity and substratum on predation by pinfish, *Lagodon rhomboides*. Turbid water decreased predation in tanks with hard substrata but had no significant effect in tanks with sand. The presence of sand reduced predation only in clear-water tanks. Burrowing by brown shrimp was reduced in turbid water which may explain this interaction. Overall, the data indicate that both turbid water and a suitable substratum for burrowing may reduce predation on brown shrimp, but the value of these refugia is highly dependent upon the species of predator.

Predation by fishes appears to be a major source of mortality of juvenile brown shrimp, *Penaeus aztecus* Ives, in estuarine nurseries. Brown shrimp spend several months as juveniles in estuaries, and analyses of the stomach contents of some estuarine fishes indicate a high incidence of predation on penaeid shrimp (see Minello and Zimmerman 1983 for review). The presence of salt marsh vegetation apparently offers shrimp protection from some of these predators (Minello and Zimmerman 1983; Zimmerman and Minello 1984), but other habitat characteristics that modify or control the extent of predator-related mortality have not been examined. Estuarine systems in the northern Gulf of Mexico are generally characterized by high turbidity and fine-grained sediments owing to an abundant supply of suspended sediment from rivers and a relatively low-energy environment (Chapman 1968; Linton 1968; Folger 1972). Production of penaeid shrimp in these estuaries is high, and the presence of turbid water together with suitable substrata for burrowing may contribute to productivity by reducing predation.

The effect of turbidity on predator-prey interactions varies with the organisms examined. In laboratory experiments with the flounder, *Platichthys flesus*, Moore and Moore (1976) found that turbid water reduced the ability of the fish to see epibenthic prey and increased the ability of prey to avoid capture. The degree of this effect varied with prey species. Gardner (1981) also found that turbidity reduced predation by bluegill, *Lepomis macrochirus*, on *Daphnia* in laboratory aquaria. Boehlert and Morgan (1985), however, found that predation rates of larval Pacific herring, *Clupea harengus pallasi*, apparently increased up to a point in turbid water. Other work in the laboratory and in freshwater lakes and streams has shown that turbidity can interact with the activity, behavior, and distribution of both predators and prey (Heimstra et al. 1969; Swensen and Matson 1976; DeVore et al. 1980; Gradall and Swenson 1982; Matthews 1984; Sigler et al. 1984), and predation rates in turbid water may be reduced or enhanced (Swenson 1978).

Burrowing by prey in the substratum may also affect predation rates, and burrowing by the crayfish, *Orconectes propinquus*, has been shown to reduce predation by smallmouth bass, *Micropterus dolomieui* (Stein and Magnuson 1976). Although experimental evidence is lacking, it has frequently been suggested that burrowing by penaeid shrimp functions in a similar manner (Williams 1958; Fuss and Ogren 1966; Hughes 1966, 1968a). Diel periodicity in the burrowing behavior of brown shrimp has been

[1]Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, Galveston, TX 77550.

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well documented (Wickham and Minkler 1975; Lakshmi et al. 1976; Minello and Zimmerman 1983), and this species generally remains beneath the surface of the substratum throughout the daylight hours, emerging to forage at night.

The objective of this search was to determine whether turbid water and a suitable substratum for burrowing affect predation rates on juvenile brown shrimp. Experiments were conducted in the laboratory, and predatory fish were southern flounder, *Paralichthys lethostigma* Jordan and Gilbert, pinfish, *Lagodon rhomboides* (Linnaeus), and Atlantic croaker, *Micropogonias undulatus* (Linnaeus). The effect of turbidity on burrowing by brown shrimp was also examined.

METHODS AND MATERIALS

Predation Experiments

Collection and Handling of Experimental Animals

Fish were collected with trawls and seines from Galveston Bay, TX, and held in clear-water tanks without a sand substratum. They were fed live shrimp daily and starved for 24 h before an experiment. Total lengths of fish were measured after each experiment, and specimens from a subsample in holding tanks were weighed and measured. A length-weight relationship was calculated and used to estimate weights of experimental fish.

Shrimp were collected by trawling 2 to 3 d before each experiment. They were fed daily with pelleted shrimp food but not fed during experiments. Measurements of total length (tip of rostrum to tip of telson) were made on all shrimp placed into experimental tanks and all shrimp removed after an experiment. A length-weight relationship was calculated for each experiment from subsamples of shrimp and used to estimate individual weights.

Experimental Tanks

Experiments were conducted in fiberglass tanks (1.75 m × 5.8 m × 0.5 m) located in a building with a white translucent roof which allowed the use of natural photoperiods. Each tank was divided in half by a wall of 1.5 mm mesh fiberglass forming two compartments (1.75 m × 2.9 m) of 5.07 m^2 bottom area. A 5 cm layer of washed beach sand (well sorted with a graphic mean grain size of 2.95 ϕ; analyzed according to Folk 1980) was placed in four tanks. In four other tanks, approximately 1 mm of sand was used to reduce the contrast between prey and the bottom of the tank. Tanks were filled to a depth of 26 cm with seawater (24-26‰) pumped from the beachfront off Galveston Island. During experiments, water temperatures varied among tanks by only 0.5°C, and diurnal ranges are listed in Table 1.

Pulverized kaolinite was used to make the water turbid in four tanks (two with sand bottoms and two without sand). Particle size analysis (Folk 1980) indicated that the kaolinite was poorly sorted with a graphic mean grain size of 8.82 ϕ. A clay slurry was introduced into tanks through a 19 L settling bucket with an outlet hose (5 mm ID) located 5 cm from the bottom. This settling bucket served to remove some of the heavier particles and flocculated aggregates from the clay suspension. Each tank contained a small submersible pump (252 L/minute capacity) connected to a discharge pipe which extended along the length of the tank and sprayed water over the surface. This pump together with 12 airstones/tank provided some vertical mixing which helped keep clay particles suspended.

Turbidity, light, and temperature were measured at 2-h intervals during each experiment. Turbidity

TABLE 1.—Design and conditions for predator-prey experiments.

Experiment	Date (1984)	Predator density[1]	No. of replicates[2]	Predator size (mm TL)	Prey size (mm)	Turbidity[3] (FTU)	Light[4] ($\mu E\ s^{-1} m^{-2}$)	Temperature (°C)
Southern flounder I	May 11	1	2	84-126	30-40	46-30	152	21.0-23.0
Southern flounder II	May 15	1	2	82-111	30-40	54-37	73	22.0-24.5
Pinfish I	May 18	3	4	62-80	30-40	53-36	48	23.0-24.0
Pinfish II	May 31	3	4	64-75	30-42	64-42	162	17.0-19.0
Atlantic croaker	June 6	3	4	98-117	30-40	58-37	132	26.0-27.5

[1]Number of predators per compartment.
[2]Number of replicate compartments used per treatment combination.
[3]Average initial and final turbidity in turbid tanks over experimental period.
[4]Average light levels measured in clear tanks over the first 5 h of the experimental period (n = 16).

was measured with an HF Instruments DRT-15 turbidimeter[2] (calibrated with a Formazin standard) and recorded as Formazin Turbidity Units (FTUs). A typical turbidity curve for acclimation and experimental periods is shown in Figure 1, and mean values from turbid tanks for each experiment are listed in Table 1. These turbidities were within the range of values measured over a 2-yr period in the Galveston Bay system (pers. obs.). Clear treatments ranged between 0.1 and 2.4 FTUs. Light levels in each tank were measured 13 cm below the surface of the water with a LI-COR integrating quantum meter (Model LI-188B) equipped with an underwater sensor. This sensor measures radiation in the 400 to 700 nm waveband, and light energy is expressed in microeinsteins ($\mu E\ s^{-1}\ m^{-2}$). Due to variability in the thickness of the roof over the experimental tanks, there were differences among the tanks in incident light reaching the surface of the water. During one experiment, light levels were measured at the water's surface, and these values were considered to be indicative of the differences among tanks during all experiments.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Experimental Design

In all experiments, there were two replicate tanks (each divided into two compartments) for each of the four treatment combinations: clear water/no sand, clear water/sand, turbid/no sand, and turbid/sand. Feeding by fish was restricted to daylight hours. Twenty-four hours before the initiation of an experiment, fish were placed in circular release cages (0.75 m diameter) within experimental compartments, and clay was then added (200 mg/L) through the settling system to four of the tanks over a 3-h period. Twenty-five brown shrimp were placed in each compartment (4.9 shrimp/m^2) approximately 15 h before the start of an experiment. At 0600 h on the day of the experiment, turbidities were measured and additional clay was added to elevate the turbidity levels and reduce variability among the four tanks. The release cages were lifted at 0700 h, and fish were allowed to feed for 12 h. The tanks were drained at the end of the experimental period, and missing shrimp were assumed to be eaten. For each experiment, two control compartments (one turbid and one clear) were stocked only with shrimp to check survival and recovery of prey.

The data were analyzed using the mean number

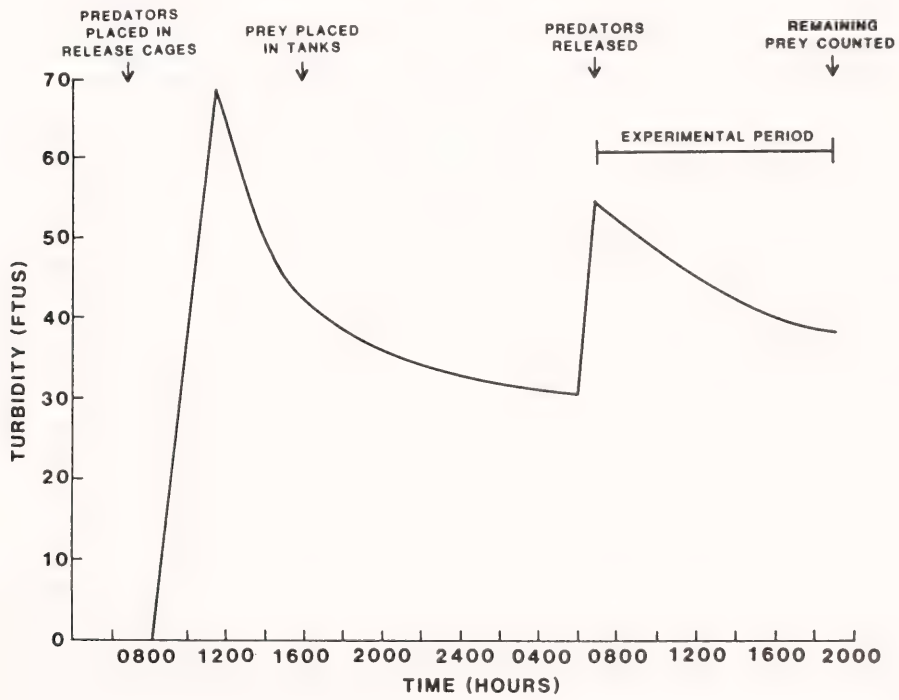

FIGURE 1.—Typical experimental sequence and turbidity (Formazin Turbidity Units) curve for predation experiments.

of shrimp eaten by a predator in a tank over the experimental period as the observation in a two-way analysis of variance (ANOVA). A second ANOVA was also performed on the weight of shrimp eaten per fish. In experiments with pinfish and Atlantic croaker, where both compartments within a tank contained predators, observations from the two compartments were considered to be within tank replicates or subsamples. With southern flounder, only one compartment was used in each tank. This experiment was repeated on a second day, and day was considered a blocking variable in the analysis. Because differences in incident light among tanks could potentially affect predation rates and increase within treatment variability, an analysis of covariance (ANCOVA) was also performed on the data from all experiments using incident light as the covariate.

The size range of shrimp available to predators was kept as narrow as possible (Table 1) to avoid problems associated with size-selective predation. In addition, we attempted to keep the distribution of shrimp within this size range similar for all replicates. The size-frequency distributions of shrimp placed in the tanks and shrimp removed from the tanks after each experiment were compared to check for evidence of size-selective predation.

Turbidity and Burrowing of Brown Shrimp

The effect of turbidity on burrowing by juvenile brown shrimp was examined in eight rectangular tanks each with a bottom area of 0.92 m^2. Water depth was maintained at 25 cm, and temperature and salinity were adjusted to 25°C and 25‰, respectively. Light was provided through white translucent skylights. Lengths of PVC pipe were installed along the walls on the bottom of each tank. The tanks were filled with washed beach sand to a depth of 5 cm, and the sand surface was approximately 5 mm below the top of the PVC pipe. The number of shrimp burrowed was determined using a net composed of fiberglass screen mounted on a wooden frame. The frame was the same width as the tanks and was pushed over the PVC runners along the bottom, passing just above the sand surface. Shrimp caught in the net were assumed to be in the water column or on the surface of the substratum.

Ten brown shrimp (50-100 mm) were placed in each tank on the day before an experiment. Before sunrise on the day of the experiment, kaolinite was added to four of the tanks through the settling bucket system. Airstones in all tanks provided enough turbulence to keep the clay in suspension. At 1100 h, turbidity and light levels were measured in the center of the water column in each tank, and nonburrowed shrimp were collected. The tanks were then drained, and the burrowed shrimp were recovered. The experiment was repeated with different shrimp on a second day, and an ANOVA, with day used as a blocking variable, was performed to test for an effect of turbidity. The percentage of shrimp burrowed in a tank was used as the observation after an arcsin transformation. The accuracy of our collecting technique was examined by comparing visual observations of the number of shrimp burrowed in the clear tanks with the catch in the net. All nonburrowed shrimp were captured in six out of seven trials, but one nonburrowed shrimp avoided capture. In one trial, a burrowed shrimp was collected.

RESULTS

Predation Experiments

Data from the two control compartments (one turbid and one clear) used in each experiment indicated that mortality of prey was low. Only 1.6% of the 250 control shrimp were not recovered alive. This mortality was considered negligible, and all shrimp not recovered in predation experiments were assumed eaten by predators. The use of a relatively narrow size range of prey also appeared to eliminate problems associated with size-selective predation. Comparisons of size-frequency distributions of shrimp introduced into experimental compartments to those removed following the experimental period showed no apparent size-selective predation in any of the experiments.

Southern Flounder

Predation by southern flounder was highest in tanks with turbid water and without sand substrata (Table 2A). The interaction term in the ANOVA was not significant, and both main effects of turbidity and substratum were significant at the 0.05 level (Table 2B). Predation rates of these fish increased from a mean of 2.2 shrimp/fish in clear water to 4.4 shrimp/fish in turbid water. Predation rates were reduced in the presence of sand from a mean of 4.8 shrimp/fish in tanks without sand to a mean of 1.9 shrimp/fish in tanks with sand. An ANCOVA with incident light and an ANOVA using the weight of shrimp eaten as the observation gave similar results. The mean weight of shrimp eaten, expressed as a

percentage of body weight eaten by the fish over the experimental period, ranged from 6.1% in clear/sand tanks to 24.8% in turbid/no sand tanks.

The feeding behavior of southern flounder (84-94 mm TL) on brown shrimp was also observed in aquaria. These fish exhibited a variety of feeding behaviors including active searching for prey on the bottom and in the water column as described by Olla et al. (1972) for summer flounder, *Paralichthys dentatus*. Generally, however, the fish remained motionless on the bottom and waited for potential prey to come within striking distance before attacking. Fish in the family Bothidae have been classified as primarily visual feeders by de Groot (1971). In our observations, all stalking activity by southern flounder was accompanied by active eye movements, tracking potential prey, which suggested the primary use of vision in prey detection. A study of diel feeding periodicity, similar to that conducted on red drum and Atlantic croaker by Minello and Zimmerman (1983), however, indicated that southern flounder could also feed at night even when tanks were enclosed in black plastic to completely eliminate light (unpubl. data). This finding suggests that sensory mechanisms, in addition to vision, can be used by these fish to detect prey.

TABLE 2.—Predation on brown shrimp by southern flounder. A) Number of shrimp eaten per fish over the 12-h experimental period for treatment combinations of turbidity and substratum. B) ANOVA results using the number of shrimp eaten per fish as the observation.

A		Turbid		Clear	
	Date (1984)	Sand	No sand	Sand	No sand
	May 11	2	4	0	4
		4	10	1	4
	May 15	1	5	2	1
		2	7	3	3
	$\bar{x}$	2.2	6.5	1.5	3.0

B	Source of error	df	SS	*F*	*P*
	Turbidity	1	18.06	5.65	0.037
	Substratum	1	33.06	10.34	0.008
	Turbidity/ substratum	1	7.56	2.36	0.152
	Day	1	1.56	0.49	0.499
	Error	11	35.19		

Pinfish

In both experiments with pinfish, the largest number of shrimp were eaten in tanks with clear water and without sand (Fig. 2). The ANOVA on the number of shrimp eaten in the first experiment (pinfish I) indicated a significant interaction between turbidity and substratum (Table 3). The substratum apparently did not affect predation in tanks with turbid water, but in clear water the presence of sand significantly reduced predation rates (Fig. 2A). In a similar manner, turbidity did not significantly affect predation in tanks with sand substrata, but it did reduce predation rates in tanks without sand. An ANCOVA with incident light and an ANOVA using the weight of shrimp eaten (Table 3) did not alter

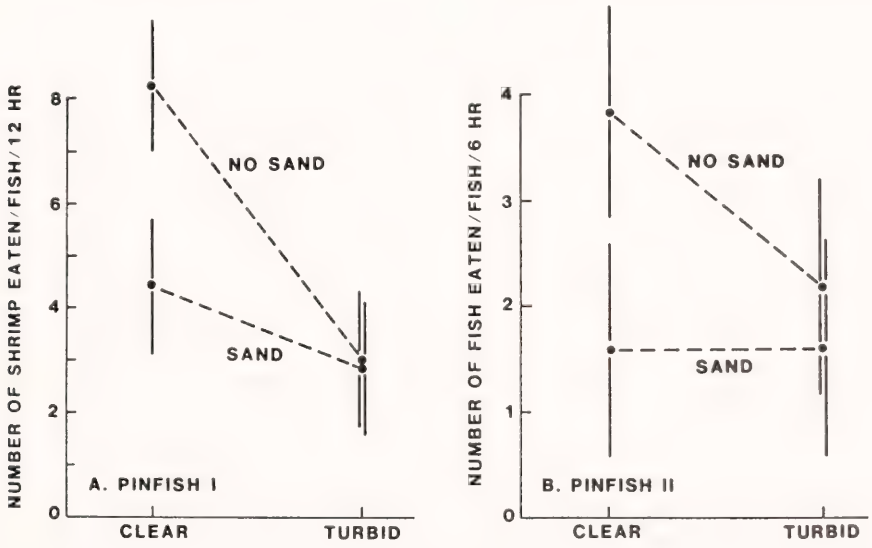

FIGURE 2.—Mean predation rates on brown shrimp by pinfish in treatment combinations of turbidity and substratum. Vertical lines, representing one half of Tukey's ω (Steel and Torrie 1960) on either side of the mean, can be used to compare means at the 0.05 significance level.

TABLE 3.—ANOVA results from predation experiments with pinfish using the number of brown shrimp eaten per fish as the observation. Probability values are also listed from an ANOVA using the weight of shrimp eaten as the observation. Turb/subs = Turbidity/substratum.

Source of error	df	SS	*F*	*P*	P (weight)
Pinfish I					
Turbidity	1	23.39	55.2	0.002	0.003
Substratum	1	8.00	18.9	0.012	0.019
Turb/subs	1	6.70	15.8	0.016	0.033
Error	4	1.70			
Pinfish II					
Turbidity	1	1.39	5.4	0.081	0.040
Substratum	1	4.00	15.5	0.017	0.040
Turb/subs	1	1.38	5.3	0.082	0.110
Error	4	1.03			
Combined					
Turbidity	1	18.10	53.1	<0.001	
Substratum	1	11.66	34.2	<0.001	
Day	1	21.81	63.9	<0.001	
Turb/subs	1	7.08	20.7	0.002	
Turb/day	1	6.68	19.6	0.002	
Subs/day	1	0.34	1.0	0.34	
Turb/subs/day	1	1.00	2.9	0.12	
Error	8	2.73			

the results. Pinfish were voracious feeders eating between 19.8% (turbid/sand) and 57.1% (clear/no sand) of their body weight in shrimp over the 12-h experimental period. Predation rates were probably underestimated in clear-water treatments without sand, since in three out of four of these compartments the three pinfish ate all of the available shrimp.

The duration of the pinfish II experiment was reduced to 6 h (0700-1300 h) to lower the overall number of shrimp eaten by the predators. Similar trends were apparent in the number of shrimp eaten for each treatment combination (Fig. 2B), but the interaction term ($P = 0.082$) in the ANOVA was not significant at the 0.05 level (Table 3). The size range of the prey in the second experiment was slightly larger than in pinfish I (Table 1), and variability in the size of shrimp available or small differences in size-selection may have affected our results. Using the weight of shrimp eaten as the observation should reduce this problem, and in this ANOVA (Table 3) both turbidity and substratum were significant effects, but the F-test for interaction had a probability value of 0.110.

To increase the error degrees of freedom and hence the power of the statistical test, the data from both pinfish experiments were combined and analyzed. In one such ANOVA, day was considered to be a blocking variable (no interaction with other factors), and the results on the number of shrimp eaten were similar to those from the pinfish I experiment, showing a significant interaction between turbidity and substratum ($P = 0.021$). We also analyzed the data in a completely randomized crossed design with day as a main effect (Table 3). In this ANOVA the turbidity/substratum interaction was highly significant, but the turbidity/day interaction was also significant indicating that the effect of turbidity on predation was less during the second experiment. In addition to the shorter duration of pinfish II, overall light levels were higher during this second pinfish experiment (clear sunny day) compared with the first experiment (overcast day) (Table 1).

Atlantic Croaker

Mean predation rates for Atlantic croaker were highest in clear-water tanks without sand, and rates in all turbid tanks were low (Table 4A). The ANOVAs with both the number (Table 4B) and weight of

TABLE 4.—Predation on brown shrimp by Atlantic croaker. A) Number of shrimp eaten per fish over the 12-h experimental period for treatment combinations of turbidity and substratum. B) ANOVA results using the number of shrimp eaten per fish as the observation. Probability values from an ANCOVA using incident light as the covariate are also included.

A

	Turbid		Clear	
Experimental tank	Sand	No sand	Sand	No sand
Tank 1 compartment 1	0	0.7	1.0	4.7
compartment 2	0	0	0.3	0
Tank 2 compartment 1	0.3	0.3	1.0	3.3
compartment 2	0.7	0	0.3	1.0
$\bar{x}$	0.2	0.2	0.7	2.2

B

Source of error	df	SS	*F*	*P*	*P* (ANCOVA)
Turbidity	1	2.92	1.8	0.251	0.027
Substratum	1	1.26	0.8	0.428	0.108
Turb/subs	1	1.26	0.8	0.428	0.943
Error	4	6.49			

shrimp eaten, however, showed no significant treatment effects. Overall, Atlantic croaker ate 2.7% of their weight in shrimp over the experimental period. Differences among tanks in incident light apparently increased the within treatment variability in the experiment. There was a significant negative linear correlation between incident light and the number of shrimp eaten in the 16 experimental compartments ($r = -0.51$, $n = 16$, $P = 0.046$). An ANCOVA using incident light as a covariate lowered the error sum of squares, and the main effect of turbidity became significant (Table 4B). This was the only experiment in which variability in incident light among tanks had a major effect on our results. Atlantic croaker appeared to feed more actively at low light levels, but predation rates were higher in clear water than in turbid water. Turbidity therefore did not appear to affect predation by simply reducing the light in the water column.

Turbidity and Burrowing of Brown Shrimp

Burrowing by juvenile brown shrimp was measured in both clear and turbid water to aid in the interpretation of significant interactions in the predation experiments. The percentage of shrimp burrowed was reduced from a mean of 85.7% in clear-water tanks to 46.9% in turbid tanks (Table 5). In the ANOVA the effect of turbidity was highly significant ($P < 0.001$). The effect of day was also significant ($P = 0.041$), and fewer shrimp burrowed on the second day of the experiment. Overall, light levels were lower on the second day, and a similar ANOVA on light measured 13 cm below the surface of the water also showed significant differences related to turbidity ($P < 0.001$) and day ($P = 0.011$). The turbidities used (30-47 FTUs) reduced the average light level in the water by 29% compared with values in clear tanks. Burrowing did not appear to be related to shrimp size, and there was no significant difference between the mean length of burrowed shrimp compared with nonburrowed shrimp (paired t-test, $P > 0.40$, 14 df).

DISCUSSION

Effect of Turbidity on Predation

Turbidity reduces predation on prey possessing limited escape capabilities by reducing the visual reactive distance of the predator (Moore and Moore 1976; Vinyard and O'Brien 1976; Gardner 1981). Turbid water should have less of an effect on predation if the predator-prey size ratio is large (Moore and Moore 1976; Vinyard and O'Brien 1976) or if the predator has the ability to use sensory mechanisms other than vision to detect prey. The significant decrease in predation rates by pinfish in our experiments may be explained in part by the strict reliance of this predator on vision for prey detection (Minello and Zimmerman 1983) and upon the relatively small predator:prey size ratio (Table 6). Turbidity appeared to have less of an effect on predation by Atlantic croaker. This predator does not depend solely upon vision for prey detection, but also uses olfaction and touch (Chao and Musick 1977). The increased predation rates for southern flounder in turbid water may be related to the ambush feeding tactics of this predator and the effect of turbidity on prey behavior. The activity level of brown shrimp increased in turbid water as evidenced by a decrease in burrowing and the frequent observation of actively swimming shrimp in turbid tanks. According to the model of Gerritsen and Strickler (1977), increased prey movement dramatically increases encounter rates with slow moving or stationary predators. This effect of prey movement is

TABLE 5.—The effect of turbidity on burrowing by juvenile brown shrimp. All measurements were taken at approximately 1100 h. Percentages of shrimp burrowed in each tank (generally 10 shrimp/tank) are listed with turbidity levels and light levels in the water column.

	Turbid tanks			Clear tanks		
Date (1984)	Burrowed (%)	Turbidity (FTU)	Light ($\mu E\ s^{-1}m^{-2}$)	Burrowed (%)	Turbidity (FTU)	Light ($\mu E\ s^{-1}m^{-2}$)
Aug. 15	56	49	51	90	5.6	89
	50	30	66	100	3.2	93
	80	42	54	80	5.9	87
	50	47	59			
Aug. 17	20	39	49	80	3.2	73
	20	32	52	90	3.2	76
	60	33	51	80	4.1	73
	40	36	51	80	2.9	46
$\bar{x}$	47.0	38.4	54.1	85.7	4.0	76.7

TABLE 6.—Summary data on possible factors affecting predation rates for the species of predators examined.

Predator	Mode of feeding	Predator searching speed (activity)	Size ratio of predator:prey[1]	Effect on predation rates	
				Turbidity	Substratum (burrowing)
Southern flounder	visual and nonvisual	low	3:1	increased	decreased
Atlantic croaker	visual and nonvisual	high	3:1	decreased	no change
Pinfish	strictly visual	high	2:1	decreased	decreased

[1]measured as total length.

reduced as predator speed increases, and changes in prey activity should only have a negligible effect on encounter rates with more active predators such as pinfish and Atlantic croaker. Increased predation rates by fish in turbid water may also be related to the effect of turbidity on the reactive distance and escape behavior of prey. The ability of the predator to detect the prey before the prey detects the predator is dependent upon differences in visual acuity, apparent size, and motion (Cerri 1983; Howick and O'Brien 1983). Although brown shrimp have the ability to visually detect predators and avoid attack, the acuity of the crustacean compound eye is much lower than that of the vertebrate eye (Waterman 1961; Goldsmith 1973), and shrimp do not respond to stationary predators. This last prey characteristic may explain why the southern flounder is a very effective predator on brown shrimp.

Effect of Substratum on Predation Rates

Juvenile brown shrimp readily burrowed in experimental tanks with fine sand substrata, but they could not burrow in tanks without sand. Burrowing should reduce the apparent density and availability of brown shrimp to visually feeding predators (Minello and Zimmerman 1984). Predators using olfactory or tactile mechanisms of prey detection, however, may have less difficulty detecting and feeding upon burrowed shrimp. Predation rates for pinfish and southern flounder, both visual feeders, were significantly reduced in tanks with sand substrata. Predation rates of Atlantic croaker were not affected by the presence of sand which suggests that burrowing does not protect brown shrimp from this predator. In other clear-water experiments conducted in our laboratory with Atlantic croaker (Albrecht et al. 1983[3]), we have been unable to detect any reduction in predation on brown shrimp related to the presence of sand substrata. This predator does not depend solely on vision to detect prey (Minello and Zimmerman 1983), and Chao and Musick (1977) hypothesized that Atlantic croaker fed mostly by olfaction and touch. These fish also search through the upper layers of the substratum while foraging for food (Roelofs 1954; Chao and Musick 1977), and this behavior may reduce the number of burrowed shrimp.

The presence of sand may also affect predation by altering the activity levels of both prey and predator. Increased activity of brown shrimp in tanks without sand may have increased encounter rates with southern flounder in accordance with the model of Gerritsen and Strickler (1977). In addition, southern flounder periodically burrow in sand, and Olla et al. (1972) found that burrowed summer flounder did not respond to the presence of prey.

Interactions Between Turbidity and Substratum

Burrowing by juvenile brown shrimp is reduced in turbid water (Table 5), and in situations where burrowing protects shrimp from predators, an interaction might be expected between the effects of turbidity and substratum on predation rates. This type of interaction was present in the pinfish experiments. Predation rates of pinfish were reduced in the presence of a sand substratum only in clear water; in turbid water predation was not significantly affected by substratum. Turbidity reduced predation in tanks without sand, but in tanks with sand substrata the effect of turbid water on feeding by pinfish was apparently attenuated by a reduction in shrimp burrowing and an increase in the number of available prey. In experiments with southern

[3]Albrecht, C., T. J. Minello, and R. J. Zimmerman. 1983. The role of substrates in predation on brown shrimp (*Penaeus aztecus*) by Atlantic croaker (*Micropogonias undulatus*). NOAA/NMFS Unpublished Report to Laboratory Director, SEFC, Galveston Laboratory, 18 p.

flounder, burrowing also appeared to reduce the number of shrimp eaten, but this reduction occurred in both turbid and clear water as evidenced by the nonsignificant turbidity/substratum interaction term ($P = 0.152$). In fact, the reduction in mean predation rates associated with the presence of a sand substratum was greatest in turbid water, and the positive effect of turbidity on predation appeared greatest in tanks without sand (Table 2A). Further analysis of the effects of turbidity and substratum on the activity of brown shrimp and the feeding behavior of southern flounder would be needed to explain interactions between these variables. Burrowing does not appear to protect brown shrimp from predation by Atlantic croaker, and there was no experimental evidence for an interaction between turbidity and substratum.

Experiments With Red Drum, *Sciaenops ocellatus* (Linnaeus)

During the course of this study two experiments were also conducted on the effects of turbidity and substratum on predation rates of another fish predator, the red drum (420-592 mm TL). An in depth analysis of these data was not included due to poor survival of shrimp in control compartments (18% of control shrimp died from unknown causes). Control mortalities, however, did not appear to be related to experimental variables, and data obtained in these experiments suggested that predation rates of red drum are not affected by turbid water or the presence of sand substrata. That substratum has no significant effect on predation rates is supported by additional unpublished but well-controlled experiments in our laboratory, indicating that burrowing does not protect juvenile brown shrimp from predation by red drum. Yokel (1966) described the feeding behavior of these fish which consists of searching along the bottom with the head down and lower jaw rubbing along the surface of the substratum. He concluded that this method of feeding would enable the fish to locate animals in shallow burrows.

CONCLUSIONS

The artificial nature of these laboratory experiments certainly must be considered when attempting to interpret the data in relation to natural phenomena. One major advantage of the apparatus used in our experiments was the relatively large size of the experimental enclosures (5.07 m^2 bottom area) which allowed the use of prey densities commonly found in natural populations. The use of these large enclosures, however, made replicating treatment combinations more difficult, hence reducing the power of statistical tests. Despite this limitation, general conclusions about relationships between turbidity, substratum, and predation on brown shrimp can be made on the basis of our experimental results. Under certain conditions, turbid estuarine water should provide juvenile brown shrimp protection from fish predators such as pinfish and Atlantic croaker. Turbidity does not appear, however, to reduce predation by southern flounder on juvenile brown shrimp. The effect of turbidity on predator-prey relationships apparently depends upon the feeding behavior and morphology of predators and on the behavior of the prey. Burrowing into the substratum also appears to protect brown shrimp from some fish predators, and the ability of brown shrimp to burrow is affected by substratum characteristics (Williams 1958; Aldrich et al. 1968; Rulifson 1981). A change from hard shell botton to soft silty mud should enhance burrowing and reduce predation by estuarine fish such as pinfish, southern flounder, and perhaps spotted seatrout. Fishes such as Atlantic croaker and red drum, however, are apparently well adapted for feeding upon burrowed organisms, and differences in estuarine sediments may not affect predation by these species. Because turbidity and substratum do not appear to alter predation of all fishes in a similar manner, the effects of these habitat characteristics on the mortality of juvenile brown shrimp should strongly depend upon the dominant fish predators present in an estuarine system.

Comparisons of estuaries with regard to their protective capacity for juvenile brown shrimp are complicated by interactions among habitat characteristics and their effects. In addition to the type of substratum, light levels (Wickham and Minkler 1975), temperature (Aldrich et al. 1968), and salinity (Lakshmi et al. 1976) have been shown to affect burrowing of brown shrimp. Starvation (Hughes 1968a), tidal movements (Hughes 1968b), shrimp size (Eldred et al. 1961; Hughes 1968a; Moctezuma and Blake 1981), and dissolved oxygen (Egusa and Yamamoto 1961) affect burrowing of other penaeids and may have a similar effect on brown shrimp. The presence of rhizomes and roots of estuarine vegetation may also reduce burrowing by these animals. All of these factors, therefore, can potentially interact with predator-related mortality. In our experiments, burrowing by brown shrimp was reduced in turbid water, and this had a significant effect on predation rates of pinfish. Interactions that control the presence of protective habitat characteristics are

also common. In low-energy areas, estuarine systems with large amounts of suspended sediments and high turbidities frequently have fine sediments (Guilcher 1967; Folger 1972). Submerged vegetation, shown to offer many crustaceans protection from predators (Nelson 1979; Stoner 1979; Coen et al. 1981; Heck and Thoman 1981), is associated with estuarine areas of low turbidity (Zieman 1982; Thayer et al. 1984), and these beds of submerged vegetation also reduce turbidity (Short and Short 1984) and alter sediment characteristics (Thayer et al. 1984). Determining the protective value of any suite of environmental characteristics, therefore, may be quite complex.

Turbidity and sediment characteristics, however, appear to be important factors governing predation rates on juvenile brown shrimp, and anthropogenic modifications of estuarine systems that influence these characteristics may affect shrimp survival. Turbidity levels and patterns of sediment deposition in estuaries are mainly influenced by riverine inputs, tidal properties, and wave action (Postma 1967; Davis 1983), although biological processes are also important (Haven and Morales-Alamo 1972; Biggs and Howell 1984). Modifications of estuarine systems through dredging, channelization, and alteration of freshwater inflows, therefore, can impact predator-prey relationships, and such effects should be addressed in evaluating these activities.

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EFFECTS OF AN EL NIÑO EVENT ON THE FOOD HABITS OF LARVAL SABLEFISH, *ANOPLOPOMA FIMBRIA*, OFF OREGON AND WASHINGTON

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ABSTRACT

The effect of El Niño conditions on the food habits of larval sablefish, *Anoplopoma fimbria*, was examined by comparing the diet of larvae collected off Oregon and Washington during the 1983 El Niño event and during 1980, a year in which conditions were not anomalous. While differential utilization of appendicularians, pteropods, and amphipods was seen in the 2 years, the most notable difference was that small copepods contributed significantly more to the diet in 1983 than in 1980. Dietary data for 1983 were generally supported by independent plankton observations, especially with respect to the predominance of *Paracalanus parvus*, a small calanoid copepod. Because adult sablefish live and spawn in deep water, changes in the food habits of neustonic larvae may represent one of the principal effects of the El Niño conditions on this species.

Larvae represent a precarious stage in the life history of marine fishes as they are highly vulnerable to fluctuations in oceanographic conditions and food resources. Their survival is dependent on successful feeding, avoidance of predation, and favorable transport (Sinclair et al. 1985). The relative importance of these factors is difficult to assess since each varies with species, developmental stage (Hewitt et al. 1985), and environmental conditions. Additionally, these sources of mortality are interactive insofar as the transport of larvae into areas with suboptimal feeding conditions may result in starvation, and starving larvae are at greatest risk for predation. Because survival past the larval and early juvenile stages clearly depends on successful feeding, understanding the success of larval populations requires a thorough knowledge of feeding ecology. As a result, in recent years a number of studies have provided detailed descriptions of the food habits of marine fish larvae (e.g., Laroche 1982; Cohen and Lough 1983; Govoni et al. 1983; Gadomski and Boehlert 1984; Brewer and Kleppel 1986), and a few studies have documented the occurrence of starvation under natural conditions (O'Connell 1980; Hewitt et al. 1985; Grover and Olla 1986; Theilacker 1986). The present study examined the food habits of larval sablefish, *Anoplopoma fimbria*, collected during 2 years of differing oceanographic conditions.

As oceanographic conditions are manifested through changes in zooplankton assemblages, between-year comparisons of the diet of larval fishes can reflect differences in oceanic conditions. Such comparisons are of particular interest when they include periods characterized by highly anomalous conditions. One such oceanographic anomaly, an El Niño event, occurred in the eastern Pacific Ocean off North America from the fall of 1982 through late summer 1983.

The magnitude of El Niño-induced anomalies in physical conditions appears to be greatest in surface waters, with anomalous conditions having the greatest effect on those life stages of fishes that occupy the upper water column. Adult sablefish inhabit deep slope waters and spawn at depths in excess of 300 m (Mason et al. 1983), and therefore may be relatively insulated from El Niño conditions (Bailey and Incze 1985). Their eggs may also be insulated, as they hatch in water deeper than 400 m (Mason et al. 1983). However, larvae ascend to surface waters where they reside through early juvenile stages (Shenker and Olla 1986; J. M. Shenker[3]). During this neustonic phase they are most vulnerable to anomalous oceanographic conditions. While El Niño con-

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ditions may affect fish larvae in several ways, Bailey and Incze (1985) speculated that sablefish may be particularly sensitive to altered food production.

The aim of the present work was to examine the effect of an El Niño event on the food habits of larval sablefish, through a comparison of their diet off Oregon and Washington during the 1983 El Niño event and 1980, a year in which oceanographic conditions were not anomalous[4]. Since an earlier study showed that prey size-selection was a function of larval size (Grover and Olla 1986), ontogenetic differences in diet were also considered.

METHODS

Sablefish larvae were collected by the cooperative U.S.–U.S.S.R. ichthyoplankton survey off Oregon and Washington, during 1980[5] and 1983[6], using a 0.5 m neuston net (Sameoto and Jaroszynski 1969) with 0.505 mm mesh towed for 10 min. Collections were made from 22 April to 4 May 1980 by the RV *Tikhookaenskiy* and from 22 April to 30 April 1983 by the RV *Ekvator* (Fig. 1). Samples with a minimum of 10 specimens were examined. A total of 267 larvae collected from 10 stations in 1980 and 136 larvae from 6 stations in 1983 were examined. In each year the number of larvae that were examined represented more than 45% of the total number of sablefish that were collected. In conjunction with neuston sampling surface water temperatures were recorded along major transects.

All larvae were preserved in 10% Formalin[7] at sea. Upon sorting they were switched into 5% Formalin, where they remained until their examination.

After the standard length (SL) of each larva was measured, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Only larvae with all or a large portion of the gut intact were examined. Gut contents were teased out, and prey items were identified: invertebrate eggs, pteropods, copepod nauplii, copepods, amphipods, euphausid larvae, appendicularians, and other prey items. When possible copepods were identified to species.

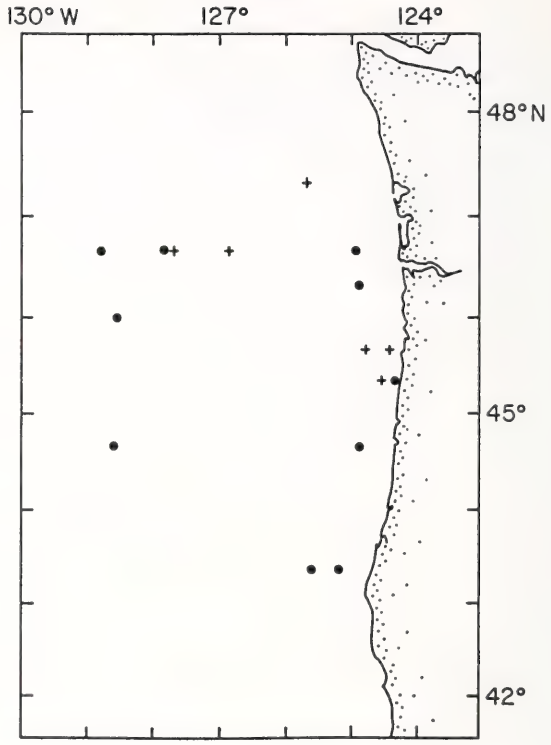

FIGURE 1.—Map of the stations off Washington and Oregon where larval sablefish were collected. Dots represent 1980 collections and crosses represent 1983 collections.

Lengths of all prey items were recorded. After the study was begun, it became clear that prey widths should also be measured. From that point on, both lengths and widths were recorded for all prey that were not dorsoventrally or laterally flattened. A conservative approach was taken with prey dimensions, i.e., prey widths excluded appendages and cephalothorax lengths were measured for copepods. Both measurements were recorded for a total of 7,508 prey items.

Diet was analyzed in terms of numerical percentage composition (%N), percent frequency of occurrence (%FO), and volumetric percentage composition (%VOL). Prey volumes were calculated from prey dimensions, assuming a spherical shape for invertebrate eggs, while all other prey were more appropriately described by a cylindrical shape. For a comparison, volumes were also calculated assuming a spheroidal shape, following Gadomski and Boehlert (1984). Regardless of whether a cylindrical or spheroidal shape was assumed, the relative contri-

[4]Sea Surface Thermal Analysis. Dates of issue: 8 May 1980 – 6 May 1986. Northwest Ocean Service Center, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115.

[5]Kendall, A. W., and J. Clark. 1982. Ichthyoplankton off Washington, Oregon and Northern California, April-May 1980. Processed Rep. 82-11, 48 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98112.

[6]Clark, J., and A. W. Kendall. 1985. Ichthyoplankton off Washington, Oregon, and Northern California, April-May 1983. Processed Rep. 85-10, 48 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

bution of each prey type was essentially the same, except that invertebrate eggs contributed slightly more (in all cases ≤0.1%) to the total volume when the spheroidal shape was assumed. After the volume of each individual prey was calculated, a median volume for each prey type was determined. Median values were used because they are free from implicit assumptions regarding the normality of these data. Each median volume was then multiplied by the raw data from the numerical percentage composition analysis to produce corresponding volumetric percent composition data. Data were examined by size group and year.

The three analyses (%N, %FO, and %VOL) were coalesced to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI = (%N + %VOL) × %FO) (Pinkas et al. 1971). For this combined analysis copepods were classified by size. Copepods <1 mm in length (TL) included *Corycaeus anglicus*, *Oithona similis*, *Oncaea* sp., *Paracalanus parvus*, and copepodites. Broken copepods of an indeterminable size were classified as unidentified small copepods. Copepods 1-2 mm long included *Pseudocalanus* sp., *Clausocalanus* spp., *Ctenocalanus vanus*, *Aedideus* sp., *Scolecithricella minor*, and *Acartia* spp. *Calanus* spp. and *Metridia lucens* were the only copepods >2 mm that were ingested.

RESULTS

Composition of the Diet of Small Larvae (≤12.5 mm SL)

During 1980, copepod nauplii comprised over 80% of the prey items ingested by number, although copepods <1 mm long contributed slightly more to the diet in terms of volume (Table 1, Fig. 2). The index of relative importance, IRI, (Pinkas et al. 1971) indicated that nauplii were more important than copepods (Table 1, Fig. 3). Many of the copepods <1 mm that were ingested by small larvae were in pieces and impossible to identify. Of those that could be identified, *Oithona similis* was the dominant species, followed by *Paracalanus parvus* (Table 2). The only noncopepod prey of much consequence was pteropods (Figs. 2, 3), locally comprising as much as 45.7% of the diet, by number.

In 1983, copepod nauplii were again the dominant prey in terms of number, but copepods represented more than twice as much in volume as they did in 1980 (Table 1, Fig. 2). While both were significant components of the diet, copepod nauplii had a slightly larger IRI value than copepods <1 mm (Fig. 3). Although the proportion of *O. similis* in the diet was similar in both years, *P. parvus* contributed more to the diet during 1983 (Table 2). A comparison of the sizes of copepods ingested during 1980 and 1983 (Table 3) showed that more small copepods were eaten in 1983, both in terms of the number of copepods ingested (χ^2 = 8.46, 1 df, $P < 0.005$) and volume (χ^2 = 755.32, 1 df, $P < 0.001$).

Composition of the Diet of Medium-Sized Larvae (12.6-20.5 mm SL)

While copepods ranked first in all analyses in 1980, other major prey items varied with method of analysis (Table 1, Fig. 2). From the IRI it is clear that copepods <1 mm were the most important prey, with *O. similis* the dominant species by number (Table 2), and *P. parvus* dominant by volume. In addition, sizable numbers of 1-2 mm copepods, especially *Acartia longiremis*, were ingested at several stations. Copepod nauplii ranked second in IRI value. Of noncopepod prey items pteropods, euphausid larvae, and appendicularians were all of consequence in the diet.

In 1983, while copepods <1 mm were again the principal prey, they comprised a greater portion of the diet than in 1980, with *P. parvus* dominating both in terms of number (Table 2) and volume. Copepod nauplii ranked second by number, but accounted for little prey volume, while euphausid larvae, the only noncopepod prey to contribute substantially to the diet, ranked higher than nauplii both in terms of volume and IRI. Of the copepod species ingested, the most striking difference between the years was the increased contribution of *P. parvus* in 1983 (Table 2).

Copepods ≥1 mm contributed more to the diet in 1980 than 1983 while small copepods comprised a greater portion of the diet during 1983 (Table 3), both in terms of number (χ^2 = 130.25, 1 df, $P < 0.001$) and volume (χ^2 = 9906.86, 1 df, $P < 0.001$).

Composition of the Diet of Large Larvae (20.6-28.5 mm SL)

While ranking second to small copepods by number and second to large copepods by volume, appendicularians comprised more than 30% of the diet by number and volume during 1980, and ranked highest in IRI value, slightly ahead of copepods <1 mm (Table 1, Fig. 3). In contrast, euphausid larvae and amphipods were the most important noncopepod prey items in the diet during 1983, although each contributed <15% to the diet. In 1983 the diet

TABLE 1.—Composition of the diet of larval sablefish in terms of the Index of Relative Importance (IRI) and its components: numerical percent composition (%N), frequency of occurrence (%FO), and volumetric percent composition (%VOL), by size class and year, with n = sample size and %ΣIRI = the contribution of each prey type to the total IRI.

Prey type	%N	%FO	%VOL	IRI	%ΣIRI
------- Larval size ≤12.5 mm -------					
1980					
Invertebrate eggs	0.5	7.9	0.1	4.7	<0.1
Pteropods	5.8	25.5	11.2	433.5	3.1
Copepod nauplii	84.0	96.4	27.1	10,710.0	77.7
Copepods <1 mm	7.4	66.1	27.8	2,326.7	16.9
1-2 mm	0.8	14.5	8.0	127.6	0.9
>2 mm					
Amphipods					
Euphausid larvae	0.4	6.7	15.3	105.2	0.8
Appendicularians	0.6	7.3	7.2	56.9	0.4
Other prey	0.5	4.2	3.3	15.6	0.1
n =	165				
1983					
Invertebrate eggs	0.5	8.2	<0.1	4.9	<0.1
Pteropods	2.1	14.3	2.7	68.6	0.4
Copepod nauplii	74.3	91.8	15.9	8,280.4	51.6
Copepods <1 mm	21.7	85.7	66.2	7,533.0	46.9
1.2 mm	1.0	18.4	5.8	125.1	0.8
>2 mm					
Amphipods					
Euphausid larvae	0.4	4.1	9.3	39.8	0.2
Appendicularians					
Other prey					
n =	49				
----- Larval size 12.6-20.5 mm -----					
1980					
Invertebrate eggs	0.3	5.1	<0.1	4.7	<0.1
Pteropods	9.4	38.0	3.7	497.8	3.9
Copepod nauplii	25.8	70.9	1.7	1,949.7	15.3
Copepods <1 mm	48.2	93.7	37.7	8,048.8	63.2
1-2 mm	7.9	49.4	19.3	1,343.7	10.5
>2 mm	0.2	3.8	5.0	19.8	0.2
Amphipods					
Euphausid larvae	2.4	25.3	18.3	523.7	4.1
Appendicularians	5.4	17.7	13.7	338.1	2.7
Other prey	0.4	3.8	0.5	3.4	<0.1
n =	79				
1983					
Invertebrate eggs	0.2	1.5	0.1	0.5	0.1
Pteropods	0.3	9.1	0.1	3.6	0.1
Copepod nauplii	9.9	60.6	0.6	636.3	3.6
Copepods <1 mm	83.3	100.0	71.6	15,490.0	88.3
1-2 mm	3.7	48.5	10.1	699.3	3.8
>2 mm	<0.1	1.5	1.1	1.8	<0.1
Amphipods	0.1	4.5	0.2	1.4	0.1
Euphausid larvae	2.3	40.9	15.7	736.2	4.2
Appendicularians	0.2	7.6	0.5	5.3	<0.1
Other prey					
n =	66				
- Larval size 12.6-20.5 mm—Continued -					
----- Larval size 20.6-28.5 mm -----					
1980					
Invertebrate eggs	2.9	13.0	<0.1	39.0	0.2
Pteropods					
Copepod nauplii	1.4	30.4	<0.1	45.6	0.3
Copepods <1 mm	40.6	95.7	13.2	5,148.7	33.1
1-2 mm	11.0	87.0	10.0	1,827.0	11.8
>2 mm	4.1	69.6	42.0	3,208.6	20.6
Amphipods	0.5	17.4	0.4	15.7	0.1
Euphausid larvae	0.9	17.4	2.2	53.9	0.3
Appendicularians	38.4	73.9	32.0	5,202.6	33.5
Other prey	0.2	8.7	0.1	2.6	<0.1
n =	23				
1983					
Invertebrate eggs	0.2	9.5	<0.1	2.8	<0.1
Pteropods	0.5	14.3	<0.1	8.6	<0.1
Copepod nauplii	0.4	19.0	<0.1	9.5	<0.1
Copepods <1 mm	71.3	95.2	24.1	9,082.1	57.6
1-2 mm	9.6	76.2	12.3	1,668.8	10.6
>2 mm	4.0	66.7	41.6	3,041.5	19.3
Amphipods	8.1	47.6	7.2	728.3	4.6
Euphausid larvae	5.5	61.9	14.3	1,225.6	7.8
Appendicularians	0.4	14.3	0.4	11.4	<0.1
Other prey					
n =	21				

shifted towards smaller copepods (Table 3), especially *P. parvus*, so that copepods <1 mm ranked highest in IRI value. Evidence for this shift came from numerical data (χ^2 = 27.30, 2 df, $P < 0.001$) as well as volumetric data (χ^2 = 1928.73, 2 df, $P < 0.001$).

A comparison of the diet of medium-sized and large larvae showed that despite other dietary differences, the number of copepods in the diet of medium-sized larvae equalled the number of copepods ingested by large larvae in 1980 (χ^2 = 0.13, 1 df, $P > 0.75$). However, large larvae ingested a greater volume of copepods in 1980 than did medium-sized larvae (χ^2 = 148.09, 1 df, $P < 0.001$). In 1983 the numbers of copepods ingested by medium-sized and large larvae were again equivalent (χ^2 = 2.93, 1 df, $P > 0.05$), although copepods contributed more, volumetrically, to the diet of medium-sized larvae (χ^2 = 657.22, 1 df, $P < 0.001$).

Comparison of Oceanographic Conditions

Because 1983 was a year of anomalous El Niño conditions, differences in diet between 1980 and 1983 may have been due to differing oceanographic conditions in the 2 years. Surface water temperatures taken during the ichthyoplankton surveys, were used as an indicator of oceanographic conditions. As the two surveys followed the same transects, station coordinates corresponded for the 2 years. Temperatures recorded from 20 April to 5 May 1980 averaged 10.67°C (s = 0.783), while those from 23 April to 6 May 1983 were significantly higher (P = 0.001) averaging 11.78°C (s = 0.772).

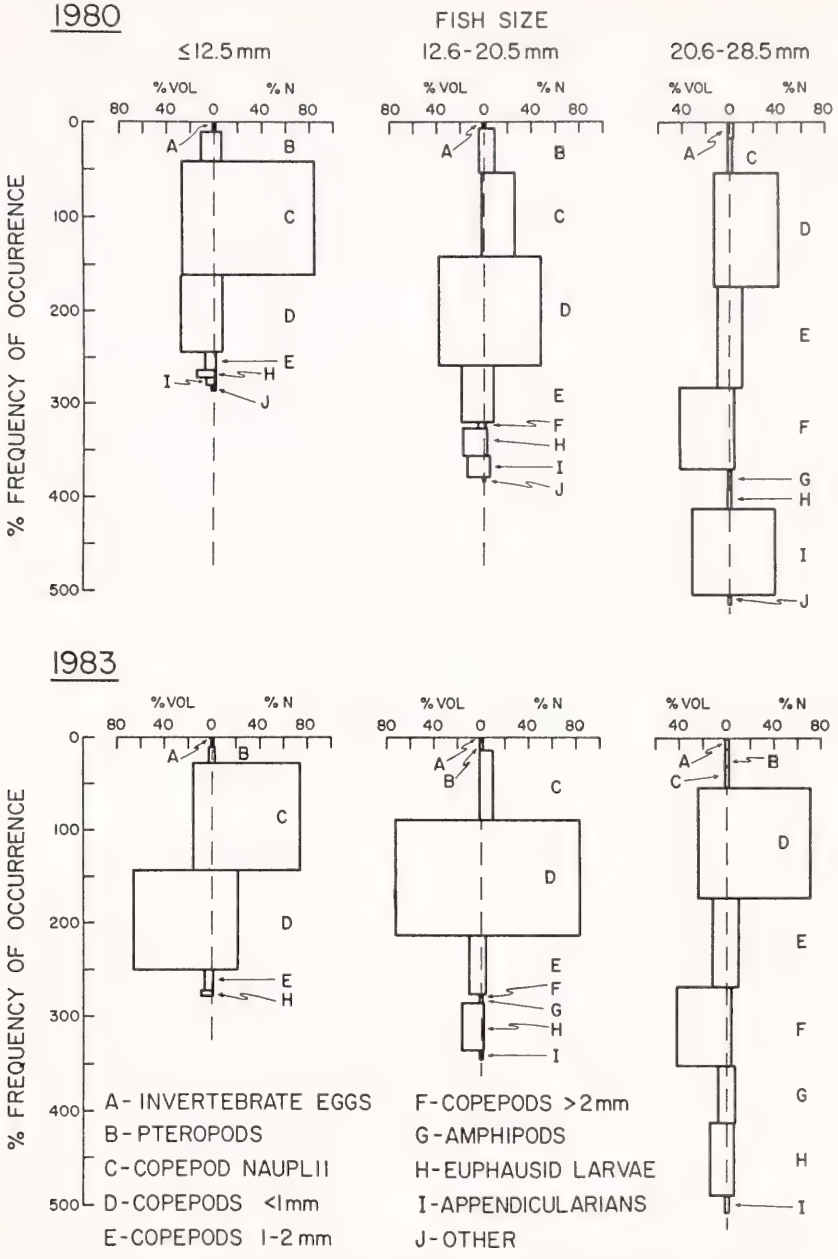

FIGURE 2.—Relative importance of prey items in the diet of larval sablefish, by size class and year, expressed as numerical percent composition (%N), volumetric percent composition (%VOL), and percent frequency of occurrence (%FO). The area of each block represents the Index of Relative Importance (IRI) of a given prey (IRI = (%N + %VOL) × %FO). Sample sizes are as listed in Table 1.

Comparisons with other years revealed that thermal patterns off Oregon and Washington were similar for 1980 through 1982 and 1984 through 1986 (fn. 4). In contrast, 1983 was markedly different, being the only year among those compared when a 13°C isotherm developed and when surface temperatures ≤10°C were not found between the coast and long. 130°W during the first week in May.

TABLE 2.—Species composition of copepods consumed by sablefish larvae. Data are expressed as numerical percentages of all copepods that were ingested by each size class in each year.

Copepod species	Larval size class (mm) ≤12.5	12.6-20.5	20.6-28.5
1980			
<1 mm			
Corycaeus anglicus		0.6	8.5
Oithona similis	27.4	38.7	16.8
Oncaea sp.	0.2	0.2	0.5
Paracalanus parvus	9.4	19.5	35.8
unidentified	38.5	19.5	8.0
copepodites	14.5	7.1	3.3
1-2 mm			
Pseudocalanus sp.	1.8	1.7	3.1
Clausocalanus spp.	1.2	2.6	2.4
Ctenocalanus vanus	5.1	1.1	4.7
Aetideus sp.			
Scolecithricella minor		0.1	
Acartia sp.	1.4	7.8	4.9
unidentified	0.5	0.8	4.7
>2 mm			
Calanus spp.		0.2	5.4
Metridia lucens		0.1	0.2
unidentified			1.7
1983			
<1 mm			
Corycaeus anglicus	0.3	0.3	1.5
Oithona similis	24.8	28.7	17.1
Oncaea sp.			
Paracalanus parvus	39.2	47.5	45.3
unidentified	23.7	13.2	15.8
copepodites	7.5	5.9	4.1
1-2 mm			
Pseudocalanus sp.	0.8	0.7	1.4
Clausocalanus spp.	0.5	0.7	3.6
Ctenocalanus spp.	2.9	1.3	1.5
Aetideus sp.		0.1	
Scolecithricella minor			
Acartia spp.	0.3	0.4	0.7
unidentified		1.1	4.2
>2 mm			
Calanus spp.		<0.1	3.4
Metridia lucens			
unidentified			1.4

TABLE 3.—Size selection of copepods by sablefish larvae. Data are expressed as a percentage of all copepods that were consumed by each size class of larvae in each year.

Copepod size	Larval size class (mm) 1980 ≤12.5	1980 12.6-20.5	1980 20.6-28.5	1983 ≤12.5	1983 12.6-20.5	1983 20.6-28.5
A. By number						
<1 mm	90.0	85.6	72.9	95.5	95.6	83.8
1-2 mm	10.0	14.1	19.8	4.5	4.3	11.4
>2 mm	0.0	0.3	7.3	0.0	<0.1	4.8
B. By volume						
<1 mm	77.8	61.0	20.3	91.9	86.5	30.7
1-2 mm	22.2	31.0	15.5	8.1	12.1	15.9
>2 mm	0.0	8.0	64.2	0.0	1.4	53.4

DISCUSSION

A comparison of the diet of sablefish larvae in 1980 and 1983 revealed several differences. Most notably, for larvae of all sizes, copepods <1 mm contributed significantly more to the diet in 1983 than in 1980. Appendicularians were the dominant prey for large larvae in 1980, but were negligible in the diet during 1983. Amphipods were only of consequence in the diet of large larvae in 1983. Pteropods comprised a substantial portion of the diet of small and medium-sized larvae in 1980, but made a trivial contribution to the diet in 1983 although ingested by larvae of all sizes.

Although concurrent zooplankton data are lacking in this study, judging from the diet, prey populations were probably quite different in 1980 and 1983. As a result of the anomalous conditions during 1983, a separate study extensively sampled zooplankton off the Oregon coast (Miller et al. 1985), where almost half (48%) of the sablefish larvae from 1983 were collected.

In both 1980 and 1983, the timing of sablefish larvae collections corresponded to the spring transitional period off Oregon reported for previous years (Peterson and Miller 1976, 1977). During this period winds and currents shift, upwelling develops, and the zooplankton is transitive between a winter assemblage that is dominated by southern species of copepods and a summer assemblage that is dominated by copepods with northern affinities. During 1980, 8% of the copepods that were ingested were northern species, representative of the spring transition, i.e., *Pseudocalanus* sp. and *Acartia* spp., especially *Acartia longiremis*. In contrast, during 1983 as a result of the El Niño event manifested through increases in surface water temperatures, sea level, and poleward currents, reductions in salinities and coastal upwelling, and a depression of the thermocline (Fiedler 1984; Huyer and Smith 1985; McGowan 1985), only a partial spring transition occurred, with southern (winter) species, especially *P. parvus* continuing to dominate the plankton through July (Miller et al. 1985). The diet during 1983 reflected this same trend with *P. parvus* being paramount in importance while northern species accounted for <1.5% of the ingested copepods.

The fact that the pteropod *Limacina helicina*, a species with northern affinities which is the dominant pteropod species off Oregon, was not very abundant in 1983 (C. B. Miller[8]) correlates well with

[8]C. B. Miller, College of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1985.

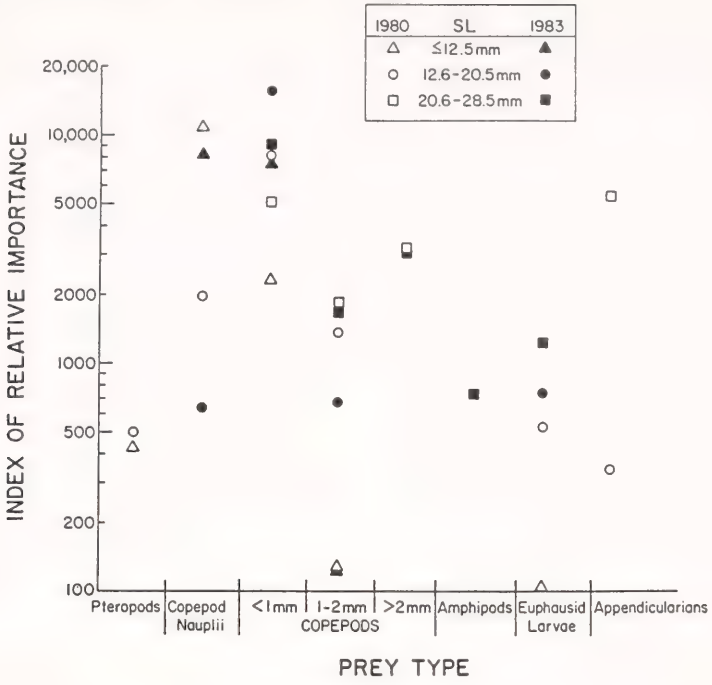

FIGURE 3.—Indices of relative importance (IRI values) of dominant prey items in the diet of larval sablefish, by size class and year. Only IRI values >100 are included. In each case the sum of IRI values <100 accounted for ≤1% of the sum of all IRI values.

our dietary observations which showed a marked decrease relative to 1980. Plankton data regarding the relative abundance of appendicularians and amphipods are less correlative with diet.

Preliminary analyses of collections made off Oregon in the spring and summer of 1983 (Miller et al. 1985) indicated that zooplankton density was reduced, possibly as low as 30% of that found in a non-El Niño year. Indirectly lending support for this was data from satellite imagery which monitored phytoplankton pigment images and which indicated that primary productivity was substantially reduced during 1983 (Fiedler 1984).

Fulton and LeBrasseur (1985) suggested that while interannual fluctuations in zooplankton biomass affect planktivorous fish living in the open ocean off the west coast of North America, major shifts in the particle size of zooplankton may have a greater effect. In particular, the extreme northward shifting of the subarctic Pacific boundary, which occurred during the 1957-58 El Niño event, resulted in the replacement of large copepods with small copepods off North America from lat. 40°N to 52°N. They hypothesized that the absence of large copepods and decreased biomass in these waters during a warm El Niño year would result in reduced growth and perhaps reduced survival of juvenile salmonids.

Ontogenetic changes in the diet of sablefish larvae included the diminution of small prey such as copepod nauplii and pteropods, and the increasing contribution of larger prey such as amphipods, euphausid larvae, and appendicularians as larvae grew. These observations parallel earlier findings on prey size-selection of larval sablefish (Grover and Olla 1986) and agree with trends seen in many other marine fish (Hunter 1981). All size classes of larvae showed some flexibility in the prey they ingested, from year to year as well as from station to station, with large larvae ingesting the widest range of prey items. The expansive range of prey ingested by large larvae may have enabled them to ingest large numbers of small copepods during 1983, when larger prey of high caloric value may not have been readily available.

From all indications, 1983 was a year of reduced planktonic productivity off Oregon and Washington (Fiedler 1984; Miller et al. 1985). It was also a year when *P. parvus*, a small copepod, was dominant both in the plankton (Miller et al. 1985) and in the diet

of larval sablefish. As low productivity and the predominance of small copepods were also observed during a previous El Niño year (Fulton and LeBrasseur 1985), these planktonic conditions may be fairly typical of El Niño events off Oregon and Washington. A comparison of the diet in 1980 and 1983 suggests that a decrease in the size of copepods ingested by sablefish larvae in 1983 may be one of the principal effects of El Niño conditions on the diet of this species. While it is possible that some energetic deficit may be imparted because of this dietary shift, the actual effects on the growth of larval sablefish are at present unknown. Although the diet in 1983 was reflective of the plankton, corresponding plankton data were not available for 1980, thus it is unclear how closely the diet resembled the plankton in 1980. However, if we assume that the copepods that were ingested by larvae are indicative of the copepods that were available, as was the case in 1983, then we may infer that larger copepods were more readily available during 1980, in the absence of anomalous conditions.

While a reduction in zooplankton biomass might affect sablefish larvae of all sizes, a paucity of large copepods would likely have the greatest effect on larvae >20.6 mm for two reasons: 1) large larvae repeatedly ingested the largest prey (Grover and Olla 1986) and 2) they were the only size class that ingested a substantial volume of large copepods.

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THE LANTERNFISHES (PISCES: MYCTOPHIDAE) OF THE EASTERN GULF OF MEXICO

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ABSTRACT

Forty-nine species from 17 genera of Myctophidae were taken in midwater trawl samples from the eastern Gulf of Mexico during March through October between 1970 and 1977. Seven abundant species (*Ceratoscopelus warmingii, Notolychnus valdiviae, Lepidophanes guentheri, Lampanyctus alatus, Diaphus dumerilii, Myctophum affine,* and *Benthosema suborbitale*) comprised 74.4% of the total number (13,369) of myctophids captured. Of the remainder, 10 species were common, 26 were uncommon, and 6 were rarely collected. Diel vertical profiles showed that all species except *Taaningichthys* vertically migrated. Daytime vertical ranges for the entire assemblage were between 300 and 900 m, while at night myctophids were most abundant between the surface and 150 m. A deep group remained below 600 m at night and was composed of mostly juvenile nonmigratory individuals of 19 species and *Taaningichthys bathyphilus*. Five daytime and five nighttime groups of associated species were defined based on vertical ranges, minimum depths of occurrence and zones of abundance. Species of tropical and tropical-subtropical zoogeographic affinities comprised the largest percentage of the total number of specimens and were about equal in their percentage contributions. The presence of many tropical species in the collections may have been due to the transport of the Florida Loop Current. Comparison of the species list with those reported for other myctophid assemblages from tropical-subtropical latitudes shows panoceanic distribution of 10 species.

Myctophid fishes are one of the dominant components of oceanic mesopelagic ecosystems (McGinnis 1974; Maynard et al. 1975; Badcock and Merrett 1976; Nafpaktitis et al. 1977; Hulley 1981; Hopkins and Lancraft 1984; Hulley and Krefft 1985). With the exception of Clarke's (1973) work in Hawaiian waters, there have been no comprehensive studies on faunal structure and ecology of this family in subtropical-tropical oligotrophic regions where myctophids are exceptionally diverse (Backus et al. 1977).

The Gulf of Mexico is one such regime. Backus et al. (1977) noted that although there are no endemic myctophid species in the Gulf of Mexico, it is zoogeographically unique and faunistically separable from other regions of the western North Atlantic. Unlike the adjacent Caribbean Sea, which it hydrographically resembles (Nowlin and McLellan 1967), the Gulf of Mexico undergoes a marked change in surface water temperatures over an annual cycle (Jones 1973). In addition, circulation patterns are strongly influenced by the Florida Loop Current, whose penetration into the Gulf of Mexico is both geographically and seasonally variable. The central Gulf of Mexico, despite seasonal variability, has many characteristics typical of low latitude oligotrophic gyre systems.

This paper details the taxonomic composition, zoogeographic affinities, and vertical structure of the mesopelagic (sensu Marshall 1971) myctophid fauna in the eastern Gulf of Mexico (hereafter as Gulf) during the warm months of late March through early October. The results are based primarily on collections with opening-closing midwater trawls made from 1970 to 1977 in the eastern central Gulf in the vicinity of lat. 27°N, long. 86°W. Additional data from other stations in adjacent northeastern and southeastern Gulf areas are included.

MATERIALS AND METHODS

The data are from 526 stations occupied during 12 cruises made between 1970 and 1977 (Fig. 1). The majority of samples were taken within a 20 nmi diameter circle centered around lat. 27°N, long. 86°W in the eastern central Gulf of Mexico, an area referred to as the "Standard Station". Samples were also taken from the northeastern and south-

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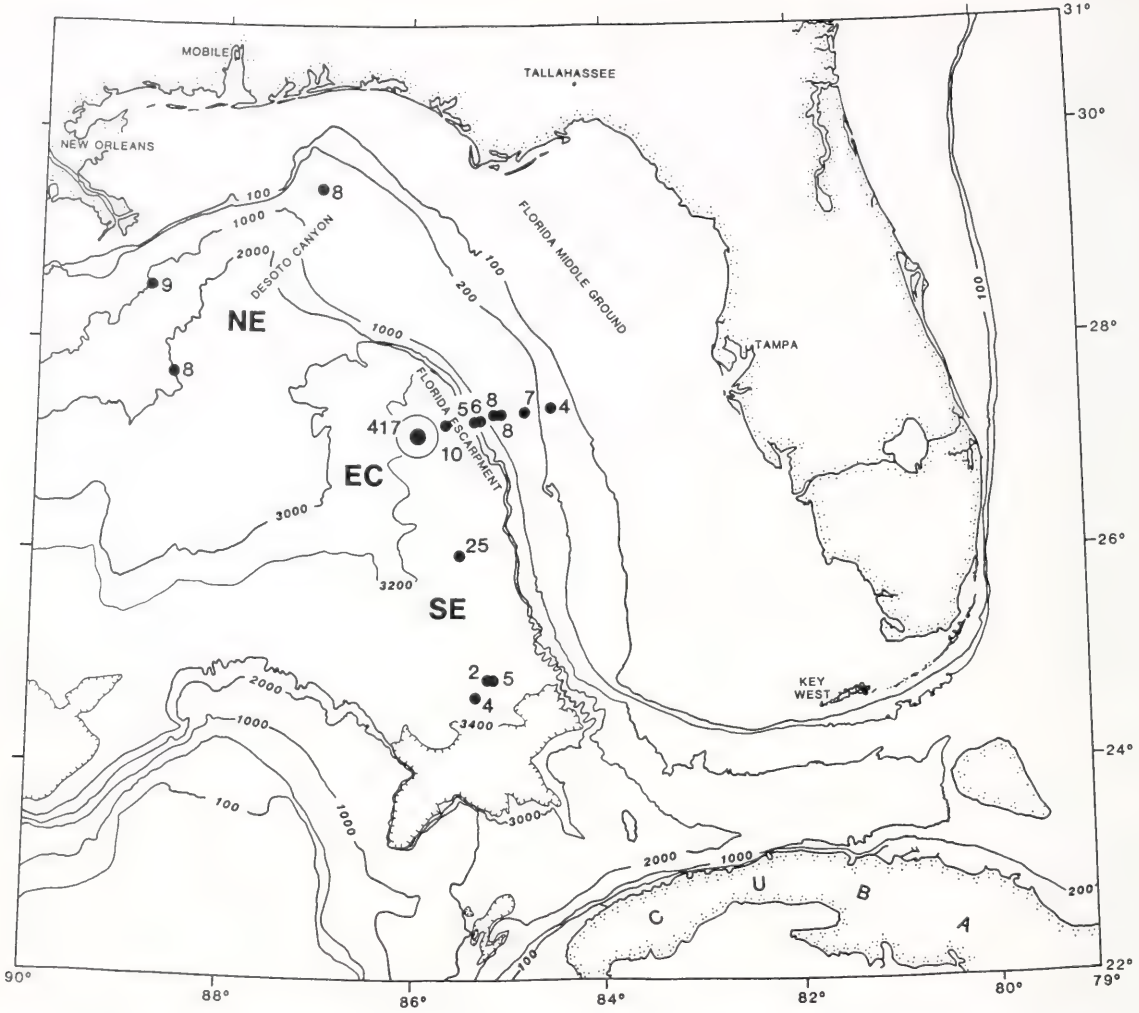

FIGURE 1.—Collection locations and numbers of tows per location in the eastern Gulf of Mexico. Sampling regions: NE - northeast; EC - eastern central; SE - southeast. Circle in EC region delimits 20 nmi diameter sampling area around lat. 27°N, long. 86°W.

eastern Gulf, and although there is a large discrepancy in the relative number of samples taken and in day-night depth coverage, collections were assigned to three latitudinal areas: northeast (NE), eastern central (EC), and southeastern (SE). The northernmost Gulf is known to support populations of cooler water myctophid species (Backus et al. 1977), and our hydrographic data showed that the southeastern stations were the only collections that were directly impacted by the tropical Loop Current waters during sampling, hence this regional partitioning.

Most of the cruises were made during the summer months (June through early September), and although sampling extended from late March through early October, all cruises were made while summer hydrographic conditions prevailed in the study area. With respect to lunar cycles, 9 of the 12 cruises occurred during waxing or full moon period, 2 during first quarter, and 1 during new moon. Table 1 lists general data for the 12 cruises.

Samples were taken primarily in the upper 1,000 m of the water column, although a few extended as deep as 1,500 m. The nets used were 3.2 m^2 or 6.5 m^2 mouth area opening-closing modified Tucker trawls (Hopkins et al. 1973) which incorporated 1.1 cm stretch mesh in the body and 505 μ mesh in the cod end. Opening and closing of the nets were accomplished mechanically using double release mechanisms and messengers. Fishing depth was

monitored on all cruises by mechanical time-depth recorders (TDR), meters of wire out and wire angle. Additionally, on three RV *Columbus Iselin* cruises (Table 1) depth was monitored by electronic deck readout via a depth transducer and conducting cable. Volume of water filtered per tow was calculated from flowmeters mounted in the mouth of the plankton net and on the main trawl frame. Inclinometer measurements and underwater observations of the wire angle of nets towed just beneath the surface indicated the mouth of the net fished at an angle of about 30° from the vertical, which was used as a standard angle when filtration volumes were calculated. Trawl speed was 1.5 to 3 kn.

Nets were fished obliquely over a depth range, or, as on *Columbus Iselin* cruises, at specific depth horizons. Vertical depth control during horizontal tows was +/−10 m from 0-300 m (except for the surface and 5 m depth strata), +/−25 m from 300-700 m, +/−50 m from 700-1,000 m.

The trawl catch was initially fixed in 10% v:v seawater Formalin[4] and subsequently transferred to 50% isopropanol. Myctophids were measured to the nearest millimeter standard length (mm SL) and identified to species using Nafpaktitis et al. (1977).

Diel vertical distributions for all species were calculated using data pooled from all cruises. Samples which were taken within 1 hour before or after sunrise and sunset were excluded from analysis, because vertical migration is pronounced at these times. Excluding the sunrise-sunset samples, a total of 155 samples (82 days, 73 nights) collected during the *Columbus Iselin* cruises from 0 to 1,000 m were used to construct vertical profiles for the abundant species (Table 2). Abundance was expressed as individuals per 10^4 m^3.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sampling data. Sampling regions: NE - northeast; EC - eastern central; SE - southeastern.

Research vessel	Date	Location/Region	No. tows (stations)	Lunar Phase[1]/Date	Loop Current impingement?
Joie de Vivre	2-5 Oct. 1970	Standard Station (EC)	12	New - 30 Sept. 1/4X - 8 Oct.	No
Dan Braman	25-31 July 1971	Standard Station (EC)	46	New - 22 July 1/4X - 30 July	No data
Mizar cruise I	7-14 June 1971	25°50′N, 85°30′W (SE)	20	Full - 9 June 3/4W - 16 June	Yes
Mizar cruise II	24-28 Mar. 1972	25°50′N, 85°30′W (SE)	5	3/4X - 22 Mar. Full - 29 Mar.	No
Bellows cruise I	2-9 Aug. 1972	Standard Station (EC)	25	1/4W - 2 Aug. New - 9 Aug.	No
Mizar cruise III	13-23 Aug. 1973	Standard Station (EC) 27°36′N, 88°40′W (NE) 29°19′N, 87°01′W (NE) 28°28′N, 88°56′W (NE)	7 8 8 9	Full - 14 Aug. 3/4W - 21 Aug.	No No No No
Bellows cruise II	9-11 Oct. 1973	24°30′N, 85°20′W (SE) 24°40′N, 85°10′W (SE) 24°38′N, 85°10′W (SE)	4 5 2	Full - 12 Oct.	Yes Yes Yes
Bellows cruise III	28-31 Aug. 1974	Standard Station (EC)	15	Full - 1 Sept.	No
Columbus Iselin cruise I	15-22 June 1975	Standard Station (EC)	79	3/4X - 16 June Full - 23 June	No
Columbus Iselin cruise II	6-17 June 1976	Standard Station (EC)	133	3/4X - 5 June Full - 12 June 3/4W - 19 June	No
Bellows cruise IV	27 May- 2 June 1977	27°11′N, 84°50′W (EC) 27°10′N, 85°07′W (EC) 27°09′N, 85°04′W (EC) 27°07′N, 85°16′W (EC) 27°06′N, 85°19′W (EC) 27°04′N, 85°40′W (EC) 27°14′N, 84°33.5′W (EC) Standard Station (EC)	7 8 8 6 5 10 4 4	3/4X - 27 May Full - 1 June	No No No No No No No No
Columbus Iselin cruise III	19 Sept. - 6 Oct. 1977	Standard Station (EC)	96	3/4X - 20 Sept. Full - 27 Sept. 3/4W - 5 Oct.	No

[1]Lunar phases: X - waxing, W - waning.

TABLE 2.—Depth horizon data for discrete-depth samples collected during *Columbus Iselin* cruises I, II, and III.

Depth (m)	Day		Night	
	No. of stations sampled	Total volume filtered (10^4 m^3)	No. of stations sampled	Total volume filtered (10^4 m^3)
0-5	16	18.4	20	24.8
10	9	5.9	3	2.0
15	5	3.4	8	2.7
30	4	3.0	3	2.0
50	6	4.5	3	3.7
75	0	—	2	3.0
105	0	—	3	4.9
125	0	—	3	3.9
155	2	2.9	2	2.6
210	1	1.5	3	3.7
300	4	6.8	3	4.6
350	4	5.1	2	2.3
400	2	2.4	2	2.8
450	5	8.0	2	2.5
500	5	4.7	3	3.7
550	3	3.0	4	5.2
600	4	11.9	1	2.5
650	2	2.6	0	—
700	3	6.6	1	2.1
800	4	7.4	0	—
900	2	4.3	2	3.7
1,000	1	2.2	3	5.9
Totals	82	104.6	73	88.6

Groups of associated species were determined for both day and night and were defined based on the minimum depth of occurrence (the shallowest discrete depth capture of a species) and zone of maximum abundance, using the *Columbus Iselin* data. These associations included the abundant and common species, as well as those uncommon species whose sample size was sufficient to determine depth range or which had a very narrow range of capture.

Although our data were limited, effects of lunar phase on vertical distribution of abundant species were examined by comparing the minimum depth of captures between new and full moon phases. Three cruises were defined as new moon (*Joie de Vivre, Dan Braman, Bellows* cruise I, Table 1); the remainder as full.

RESULTS

Hydrography

The circulation of the eastern Gulf of Mexico is dominated by the Loop Current (Leipper 1970; Nowlin 1971; Jones 1973; Molinari and Mayer 1980). This current, of Caribbean origin, enters the Gulf through the Yucatan Straits and moves anticyclonically, exiting through the Florida Straits. The extent of penetration into the Gulf is latitudinally variable and seasonally unpredictable. The Loop Current can be identified by the depth of the 22°C or 20°C isotherms which occur at 100 m and 150 m, respectively (Leipper 1970; Maul 1977; Sturges and Evans 1983). Meanders of the Loop Current often pinch off to form cold core eddies which spin cyclonically and drift southward along the eastern edge of the Loop Current off the West Florida Shelf (Vukovich and Maul 1985). Some of these cyclonic eddies have been tracked through our eastern sampling areas (EC and SE).

All of the southeastern (SE) collections were in waters covered by the Loop Current at the time of sampling, whereas the more northerly samples (EC and NE) were from what is termed Loop Transition Water. The characteristics of Loop Transition Water during the collection period (summer) were as follows: a mixed layer of variable depth, usually extending 25 to 50 m with surface temperatures of 27° to 30°C; a sharp thermocline from the base of the mixed layer to approximately 150 m depth where the temperature was 15° to 18°C; a gradual temperature decline from 150 m to about 4°C at 1,000 m. Figure 2 illustrates a typical profile of the Loop Transition Water during the summer months.

Productivity measurements within the Loop Current and in Loop Transition Waters indicate an

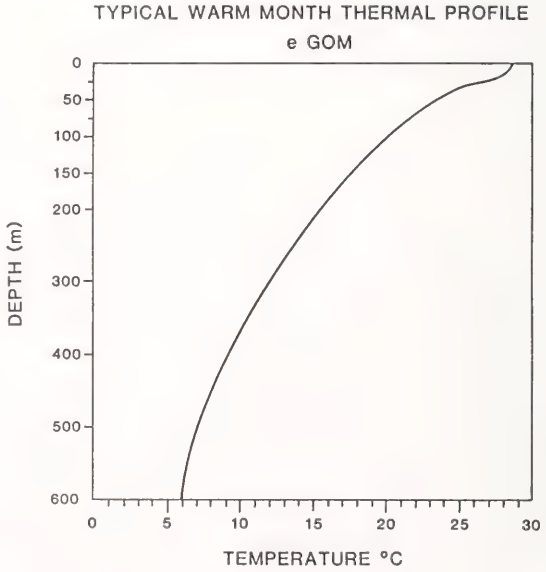

FIGURE 2.—Typical warm month thermal profile for the eastern Gulf of Mexico (eGOM).

oligotrophic regime in the eastern Gulf, with an annual primary production of <50 to 75 g C yr^{-1} (El-Sayed 1972; Hopkins 1982, unpub. data).

Species Data

A total of 13,369 myctophids were examined from all stations, with all but 77 (0.6%) identifiable to species. Table 3 lists all taxa, along with the number of individuals captured from each sampling region, their distribution pattern (from Backus et al. 1977), diel distribution ranges, and overall size ranges. The identified material comprised 17 genera and 49 species.

The distribution ranges and estimates of abundance and standing stock of the abundant species in the following species accounts were limited to data collected during the three *Columbus Iselin* cruises to Standard Station (EC). Too few collections were made in the other two areas (NE, SE) to allow for comparable analyses.

Based on frequency of capture and total number of specimens from EC, seven species were considered abundant, i.e., dominant, (>500 specimens total captured) in the eastern Gulf. In decreasing order of abundance these were *Ceratoscopelus warmingii*, *Notolychnus valdiviae*, *Lepidophanes guentheri*, *Lampanyctus alatus*, *Diaphus dumerilii*, *Benthosema suborbitale*, and *Myctophum affine*. Together they comprised approximately 75% of the total number of specimens collected from EC (74.4%). Table 4 lists the dominant species along with their percentage composition among the dominant species and overall.

From all collections, 42 additional species were divided into the following abundance categories: common (101-500 specimens; 10 species); uncommon (10-100 specimens; 26 species), and rare (<10 specimens; 6 species).

Abundant Species

Ceratoscopelus warmingii: N = 2,267, 14-65 mm SL, Juvenile-Mature Adult

The vertical distribution profile shows this species to be a strong migrator with a broad diel depth range (Fig. 3a). During the day, it occurred from 650 to 1,000 m (recent deep mesopelagic daytime tows in the Gulf of Mexico have taken *C. warmingii* below 1,000 m, J. V. Gartner unpub. data). Night captures were mainly between 75 and 125 m, with a maximum abundance of 95 individuals/10^4 m^3 at 125 m. Abundance was bimodally distributed with some small juveniles apparently remaining near daytime depths at night (Fig. 3a, Table 5).

Notolychnus valdiviae: N = 1,780, 9-22 mm SL, Postlarvae-Mature Adult

Peak daytime distribution was mainly between 400 and 500 m (Fig. 3b). Some night captures were made as shallow as 50 m, but abundance maxima were found at 75 and 155 m, with the peak at 75 m (>72 individuals/10^4 m^3). The distribution pattern was discontinuous, with no specimens taken at 125 m. There was no evidence for a nonmigratory portion of the population as was found for *C. warmingii*.

Analysis of the size vs. depth for *N. valdiviae* showed an increase in mean size with increasing depth at night (Table 5). No trend was apparent during the day because of small sample size.

Lepidophanes guentheri: N = 1,610, 13-64 mm SL, Juvenile-Mature Adult

This species was a moderate to strong vertical migrator. Although daytime captures were recorded as shallow as 400 m, this species was most abundant between 650 and 800 m and recent discrete depth hauls in the Gulf of Mexico have also taken *L. guentheri* from below 1,000 m (J. V. Gartner unpub. data). Nighttime abundance was highest at 75 m (38.1 individuals/10^4 m^3) and sharply decreased below this depth (Fig. 3c). Differences in day-night abundances were not as pronounced as in *Ceratoscopelus* or *Notolychnus*. At 650 m during the day, catch abundance was approximately the same as at 105 and 125 m at night.

Lepidophanes guentheri was the only abundant species for which lunar influence on depth of capture was apparent. During a new moon cruise (*Dan Braman*), *L. guentheri* measuring 27 to 37 mm SL were captured as shallow as 10 m.

Nonmigration of members of the population was noted, mostly among juveniles measuring from 13 to 25 mm SL. Because of sample size, no other clear size-depth patterns were discernible.

Lampanyctus alatus: N = 1,418, 15-48 mm SL, Juvenile-Mature Adult

The daytime vertical profile extended from 350 to 900 m, with a peak at 650 m (Fig. 3d). This species was found between 75 and 155 m at night (maximum 24.2 individuals/10^4 m^3 at 125 m). Some estimated daytime abundances for *L. alatus* were as large as

TABLE 3.—List of species grouped according to abundance. Totals by region, zoogeographic affinity, diel vertical depth and peak abundance ranges and size ranges. Sampling regions: NE - northeast; EC - eastern central; SE - southeastern.

Species	Region				Distribution pattern[1]	Day		Night		Size range (mm SL)	Non-migrators?[2]
	Total	NE	EC	SE		Range (m)	Max. (m)	Range (m)	Max. (m)		
Abundant											
Benthosema suborbitale	687	159	467	61	TST	400-600	—	50-105;500-550	—	10-30	Yes
Ceratoscopelus warmingii	2,267	338	1,872	57	TST	650-1,000	—	75-125;600-700	75,125	14-65	Yes
Diaphus dumerilii	1,279	273	970	36	T	300-600	—	50-155	75,125	12-53	No
Lampanyctus alatus	1,418	240	1,143	35	T	350-900	650	75-155	125	15-48	No
Lepidophanes guentheri	1,610	128	1,305	177	T	400-900	650	75-155;700-1,000	75	13-64	Yes
Myctophum affine	893	20	865	8	T	500	—	Surface-155	Surface	12-58	No
Notolychnus valdiviae	1,780	364	1,213	203	TST	400-500;800	400	50-155	75	9-22	No
Common											
Bolinichthys photothorax	130	16	105	9	TSST	550-700	—	50-250	90-125	12-51	No
Centrobranchus nigroocellatus	104	3	101	—	TST	400-550	—	Surface-150	Surface	13-43	No
Diaphus lucidus	131	14	101	16	T	450-1,000	450-600	60-300	100-150	15-79	No
D. mollis	434	72	340	22	TST	300-1,000	400-550	50-225;450-500	50-100	9-53	Yes
D. problematicus	105	15	78	12	T	325-550	400-500	55-275	80-150	15-73	No
D. splendidus	307	8	288	11	TSST	300-600	400-550	30-250;450-550	50-110	11-64	Yes
Diogenichthys atlanticus	121	24	95	2	TST	350-700	550-600	50-220;650-700	65-125	9-23	Yes
Hygophum benoiti	463	64	388	11	TmpSST	300-700	550-600	0-250;500-700;1,000	50-125	10-43	Yes
H. taaningi	362	34	286	42	ST	350-1,000	500-700	10-300;375-600	75-130	11-47	Yes
Lampanyctus lineatus	171	16	149	6	ST	600-1,000	—	110-600;800-1,000	110-300	25-113	Yes
Uncommon											
Bolinichthys supralateralis	49	15	28	6	TST	250-600	—	60-250;500-700	—	12-44	Yes
Diaphus brachycephalus	56	3	31	22	TSST	350-600	—	50-300	125-200	9-40	No
D. effulgens	14	1	11	2	ST	300-500	—	110-330?	—	10-48	N/D
D. fragilis	14	2	10	2	T	350-550	—	70-200	—	10-69	N/D
D. garmani	17	3	8	6	T	350-550?	—	65-150	—	11-28	N/D
D. luetkeni	72	14	54	4	T	300-600	—	60-300	100-160	10-52	No
D. perspicillatus	36	8	18	10	T	300-600	—	40-140	40-75	11-36	N/D
D. rafinesquii	45	2	43	—	TmpSST	300-600	400-500	100-375;500	100-150	11-80	Yes
D. subtilis	25	2	20	3	TSST	400-600	—	100-325;450-475	—	11-50	Yes
D. taaningi	41	23	15	3	P	400-550?	—	40-300	40-75	15-56	No
D. termophilus	16	2	14	—	T	—	—	75-150	—	10-35	N/D
Gonichthys cocco	34	2	30	2	TST	—	—	Surface;100-150	Surface	20-49	N/D
Hygophum macrochir	34	3	20	11	T	500-650	—	10-250	50-100	13-35	No
H. reinhardtii	82	11	70	1	ST	550-700	—	0-250;600-900	100-150	12-49	Yes
Lampadena luminosa	94	18	71	5	TSST	500->1,000	600-650	65-350;550-600	75-125	17-85	Yes
Lampanyctus ater	35	14	19	2	ST	500?-650	—	100-350;500-700	—	25-95	Yes
L. cuprarius	15	1	13	1	ST	600-900	—	125-220;600-950	—	22-61	Yes
L. nobilis	52	1	46	5	T	800-1,000	—	40-250;600	100-150	19-78	Yes
L. tenuiformis	24	5	19	—	T	—	—	75-250?	100-150	19-53	N/D
Lobianchia gemellarii	76	14	52	10	TST	300-450	—	80-210	70-125	12-48	No
Myctophum asperum	27	2	25	—	T	400	—	Surface-150	Surface	14-35	N/D
M. nitidulum	18	—	18	—	TST	—	—	Surface-50;600	Surface	16-77	Yes
M. obtusirostre	32	6	24	2	T	500-600	—	Surface-150	Surface	11-37	N/D
M. selenops	20	—	19	1	TST	—	—	60-150	—	10-43	N/D
Notoscopelus resplendens	69	1	65	3	TST	—	—	50-225	75-125	19-57	No
Taaningichthys bathyphilus	11	—	10	1	B	600->1,000	—	900	—	18-56	Yes

TABLE 3.—*Continued.*

Species	Region				Distribution pattern[1]	Day		Night		Size range (mm SL)	Nonmigrators?[2]
	Total	NE	EC	SE		Range (m)	Max. (m)	Range (m)	Max. (m)		
Rare											
Diaphus bertelseni	1	—	—	1	TST	—	—	160-190	—	10-46	N/D
Hygophum hygomii	8	—	7	1	TmpSST	—	—	50-100	—	8-44	N/D
Notoscopelus caudispinosus	8	—	7	1	TST	—	—	60-150	—	20-68	N/D
Symbolophorus rufinus	3	1	2	—	TST	—	—	50-250?	—	13-28	N/D
Taaningichthys minimus	1	1	—	—	ST	>600	—	—	—	N/D	N/D
T. paurolychnus	1	—	1	—	B	>1,000	—	—	—	54	N/D

[1]Pattern determined from Backus et al. (1977). Abbreviations are as follows: T - Tropical; TST - Tropical-Subtropical; TSST - Tropical-Semisubtropical; ST - Subtropical; TmpSST - Temperate-Semisubtropical; P - Pseudooceanic; B - Bathypelagic.
[2]Refers to nonmigration of members of the population. N/D indicates insufficient data for determination.

some of those for night, though overall densities were higher for night. No evidence was found for members of the population remaining at depth at night.

Diaphus dumerilii: N = 1,279, 12-53 mm SL, Juvenile-Mature Adult

This species had the shallowest daytime depth of capture (300 m) and was the weakest migrator of all seven abundant species (Fig. 4a); maximum depth during the day was 600 m, with no discernible abundance peak within the daytime range. Nighttime captures were as shallow as 50 m, with peak abundance between 75 and 125 m (maxima 39 and 47 specimens/10^4 m^3, respectively). There was some evidence of nonmigration of juvenile members of the population remaining at depth at night (Table 5).

Myctophum affine: N = 893, 12-58 mm SL, Juvenile-Mature Adult

Our only discrete record of capture for this species during the day was from 500 m. The nighttime vertical profile for *M. affine* was distinctly different from that of the other abundant species. A strongly bimodal pattern was evident, with a 75-155 m component of the population with a small peak at 105 m, and the majority of the population at night (97% of our catch) between the surface and 5 m. Most of these shallow individuals were at the surface (95% of 0-5 m captures), and on calm nights, it was possible to dip net this species. A maximum of 102 specimens/10^4 m^3 was recorded at the surface at night (Fig. 4b), and our data indicated that the entire population vertically migrated.

Analysis of *M. affine* size with depth for night-captured individuals showed that in the 0 to 5 m depth strata, juveniles of 18.5 mm mean SL entered the very surface waters, while specimens approximately twice their size ($\bar{x}$ = 37.2 mm SL) occurred just below them at 5 m depth (Table 5).

Benthosema suborbitale: N = 687, 10-30 mm SL, Juvenile-Mature Adult

The daytime depth range was well defined between 400 and 600 m. Nighttime distribution was bimodal, with a migratory group between 50 and 105 m and a group of nonmigratory juveniles (Table 5) remaining at daytime depths. The diel vertical profile showed that this species was not particularly concentrated at any depth (Fig. 4c) and, in contrast to all other abundant and common species, *B. sub-*

TABLE 4.—Abundance data for dominant myctophid species from the eastern Gulf of Mexico. CI - Columbus Iselin cruises I, II, III; other - all other cruises.

Species	Number captured CI (other)	Dominant species (%)	Total species (%)
Ceratoscopelus warmingii	1,822(445)	22.8	17.0
Notolychnus valdiviae	1,169(611)	17.9	13.4
Lepidophanes guentheri	1,124(486)	16.2	12.1
Lampanyctus alatus	942(476)	14.3	10.7
Diaphus dumerilii	846(433)	12.9	9.6
Myctophum affine	646(247)	9.0	6.7
Benthosema suborbitale	419(268)	6.9	5.2
		Total	74.7

orbitale was somewhat more prevalent in our day than our night catches.

Common Species

Ten species were represented by 101 to 500 specimens (Table 3). With the exception of two species (*Lampanyctus lineatus* and *Diaphus lucidus*), sizes ranged from postmetamorphic through sexually mature adult stages. The maximum sizes for all 10 species, however, were smaller than reported in Nafpaktitis et al. (1977).

Diel distribution patterns showed that all species in this group were migrators (Table 3). During the day, the maximum abundance of all but one species occurred between 400 and 700 m. *Lampanyctus lineatus* was found between 600 and 1,000 m.

At night, three vertical patterns were evident. *Centrobranchus nigroocellatus* entered the surface (0-5 m) waters, while *L. lineatus* remained at lower epipelagic-upper mesopelagic depths (110-300 m). The other eight species primarily concentrated between 50 and 150 m, though *Hygophum benoiti* and *H. taaningi* were often captured as shallow as 0 to 10 m, which suggests that these species may have disjunct night distributions similar to *Myctophum affine*.

The entire populations of *Diaphus lucidus, D. problematicus, Bolinichthys photothorax,* and *Centrobranchus nigroocellatus* apparently migrated nightly while some individuals of the other six species remained at depth at night (Table 3). Data were insufficient to discern size-depth trends in these species.

Uncommon and Rare Species

Twenty-six uncommon species were represented by 10 to 100 specimens in our collections. Comparison of the sizes captured vs. size at metamorphosis and sexual maturity (where known) indicated that six species (*Lampadena luminosa, Lampanyctus ater, L. cuprarius, L. nobilis, L. tenuiformis, Notoscopelus resplendens*) were represented only by juveniles. Nine species (*Bolinichthys supralateralis, Diaphus effulgens, D. perspicillatus, D. subtilis, D. termophilus, Hygophum macrochir, Myctophum asperum, M. obtusirostre, M. selenops*) occurred only

TABLE 5.—Mean size (mm SL) of dominant species with respect to depth.

Depth (m)	*Ceratoscopelus warmingii*		*Notolychnus valdiviae*		*Lepidophanes guentheri*		*Lampanyctus alatus*		*Diaphus dumerilii*		*Myctophum affine*		*Benthosema suborbitale*	
	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night	Day	Night
0												18.5		
5												37.2		
10														
15														
30														
50				12.0						15.0		15.0		12.0
75		25.1		16.9		43.2		20.6		24.0		17.0		21.5
105		44.3		17.4		53.4		37.8		35.9		27.8		25.0
125		32.3				51.3		35.4		26.2		23.5		
155				17.4		59.0		41.8		35.0		27.0		
210														
300									14.2					
350														
400			18.0		52.0		23.0		22.5				28.5	
450			18.7						16.0				18.0	
500			16.7				24.0				16.0		19.7	
550					23.0		23.0			18.0			28.0	10.3
600		27.0			59.0		34.0		12.0				30.0	
650	14.0				31.4		37.0							
700	16.5	15.5			44.5	14.0	37.6							
800	36.5		20.0		32.8		30.0							
900	30.5				19.0	54.0	44.0							
1,000						21.3								

as newly metamorphosed through juvenile stages (Table 3). The remaining 11 species showed a relatively complete ontogenetic series. With the exception of *Hygophum reinhardtii*, no individuals of the 26 uncommon species approached the maximum size recorded for these species (Nafpaktitis et al. 1977).

During the day, most species were found between 300 and 700 m, except for *Lampanyctus cuprarius*, *L. nobilis*, *L. tenuiformis*, and *Taaningichthys bathyphilus*, which generally were captured deeper than 600 m. Nocturnal vertical patterns showed that all uncommon species except *Taaningichthys*, a nonmigrator, entered upper mesopelagic or epipelagic depths at night. *Gonichthys cocco*, *Myctophum*

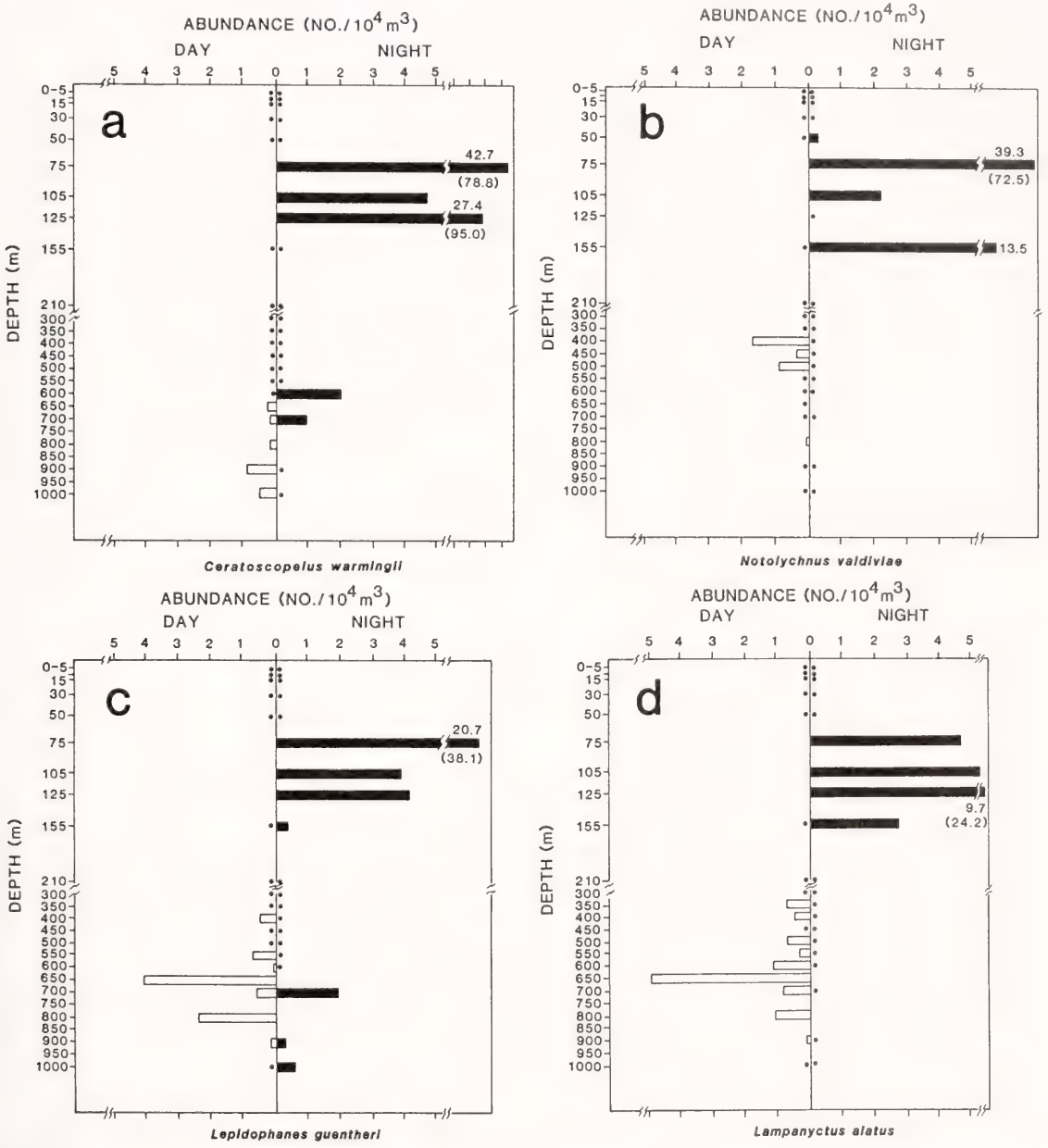

FIGURE 3.—Diel vertical profile of dominant myctophid species in the eastern Gulf of Mexico. a - *Ceratoscopelus warmingii*; b - *Notolychnus valdiviae*; c - *Lepidophanes guentheri*; d - *Lampanyctus alatus*. Numbers above bar indicate average abundance at depth, numbers in parenthesis below bar indicate maximum abundance at depth.

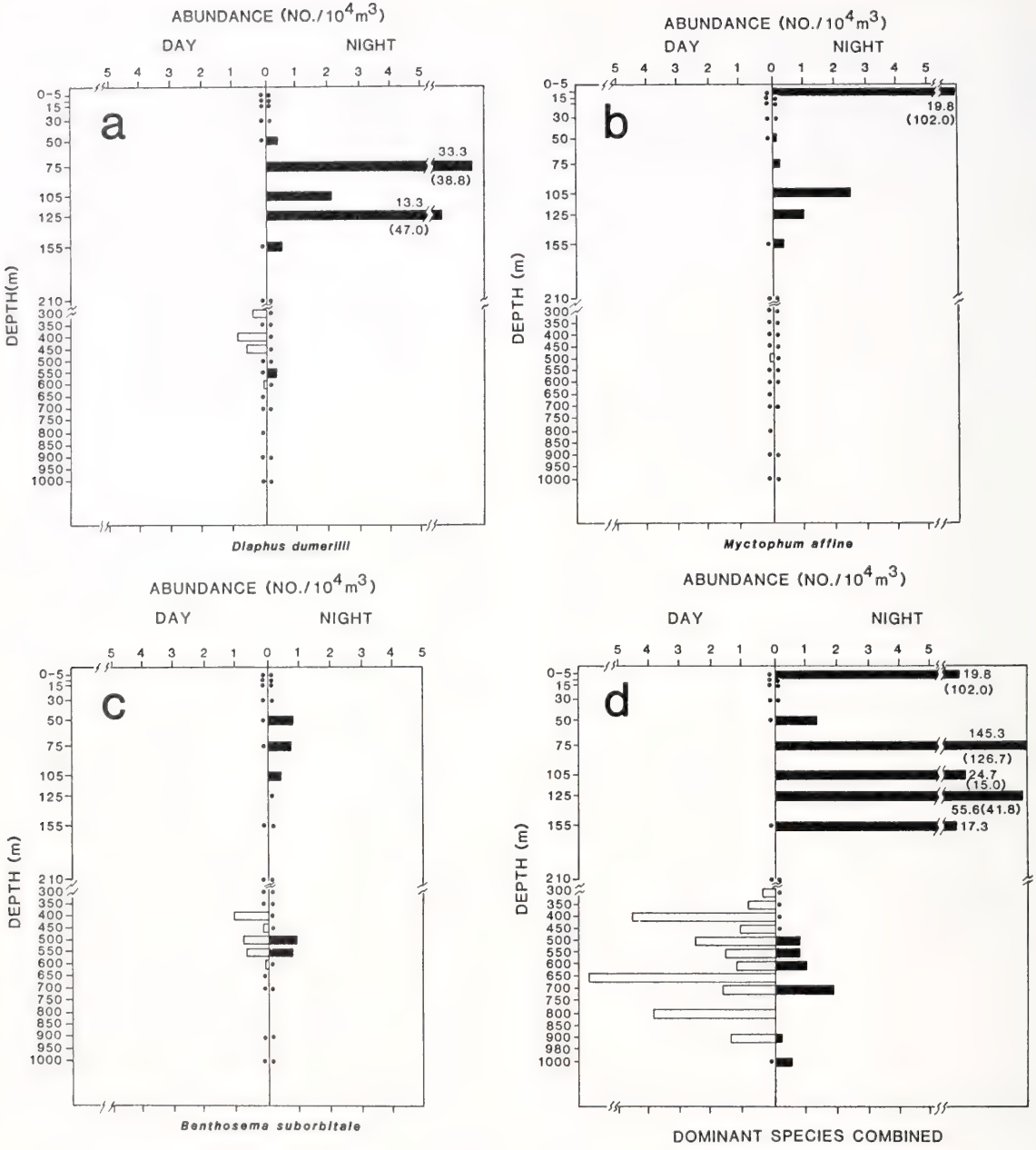

FIGURE 4.—Diel vertical profile of dominant myctophid species in the eastern Gulf of Mexico. a - *Diaphus dumerilii*; b - *Myctophum affine*; c - *Benthosema suborbitale*; d - All dominant species (7) combined. Numbers above bar indicate average abundance at depth, numbers in parenthesis below bar indicate maximum abundance at depth.

asperum, *M. nitidulum*, and *M. obtusirostre* were most abundant in the surface (0-5 m) strata. *Hygophum macrochir*, which also entered near surface waters, *Diaphus perspicillatus*, *D. taaningi*, and *Myctophum selenops* occurred primarily between 50 and 100 m. Seven species (*Bolinichthys supralateralis*, *Diaphus fragilis*, *D. garmani*, *D. termophilus*, *Lampadena luminosa*, *Lobianchia gemellarii*, *Notoscopelus resplendens*) were most abundant between 75 and 150 m. The remaining 11 species usually were found deeper than 100 m, although several (*Diaphus brachycephalus*, *D. luetkeni*, and *Lampanyctus*

nobilis) were captured as shallow as 50 m, and *Hygophum taaningi* was occasionally taken in surface (0-5 m) waters. Individuals of nine species were taken deep at night, between 450 and 950 m, indicating incomplete migration of the populations (Table 3).

Six species were considered rare (<10 individuals). Both *Taaningichthys* species were taken below 600 m during the day while the other four species came primarily from night samples between 50 and 200 m (Table 3).

NE and SE Sampling Areas

A total of 1,943 specimens from 42 of the 49 eastern Gulf myctophid species were captured in the NE sampling area, while 40 of the 49 species were recorded from SE samples (813 specimens; Table 3). The seven most abundant species in both areas are the same as for EC with the exception of *Myctophum affine*, which was infrequently captured because of a lack of surface night samples. *Diaphus mollis* was in the top seven species in the NE locale; *Hygophum taaningi* in the SE. The top seven species comprised 81.0% of the total number of specimens collected from NE samples and 75.2% from SE.

DISCUSSION

Vertical Distribution

Despite spatial overlapping, the vertical profiles of the eastern Gulf of Mexico myctophids show discrete stacking of species groups, which presumably enhances partitioning of spatial and trophic resources. Based on minimum depths of occurrence (MDO), vertical ranges and zones of abundance, groups of clearly associated species can be defined (Table 6). Five day and five night groups were constructed. Each day group consists of at least one abundant species plus one or more common species. However, because of differential migration ranges, only the three shallowest night groups contain abundant species.

During the day, almost all species have an MDO within their zone of highest abundance. All *Diaphus* species are typically upper mesopelagic inhabitants, while *Lampanyctus* and *Taaningichthys* species primarily dwell in the lower mesopelagic zone. *Hygophum* and *Myctophum* species are divided among upper and middle zones.

The daytime distribution of the abundant species

TABLE 6.—Species groups based on minimum depth of occurrence (MDO) and zones of abundance by day (36 spp.) and night (43 spp.). Underline indicates abundant species. Species in parentheses are outside of zone of maximum abundance; number after name indicates zone.

MDO (m)	Species		MDO (m)	Species	
	DAY			NIGHT	
300	*B. supralateralis*	*D. problematicus*	Surface	*C. nigroocellatus*	*M. affine*
	D. dumerilii	*D. rafinesquii*		*G. cocco*	*M. asperum*
	D. effulgens	*D. splendidus*		(*H. benoiti*; 50-125)	*M. nitidulum*
	D. luetkeni	*H. benoiti*		(*H. macrochir*; 50-100)	*M. obtusirostre*
	D. mollis	*L. gemellarii*		(*H. reinhardtii*; 100-150)	
	D. perspicillatus			(*H. taaningi*; 75-130)	
350	*D. brachycephalus*	*D. atlanticus*	50	(*B. photothorax*; 90-125)	*D. perspicillatus*
	D. fragilis	*H. taaningi*		*B. supralateralis*	(*D. problematicus*; 80-150)
	D. garmani	(*L. alatus*; ⩾600)		*B. suborbitale*	*D. splendidus*
400	*B. suborbitale*	*D. taaningi*		(*D. brachycephalus*; 125-200)	*D. taaningi*
	C. nigroocellatus	(*L. guentheri*; ⩾600)		*D. dumerilii*	(*L. nobilis*; 100-150)
	D. lucidus	*N. valdiviae*		(*D. lucidus*; 100-150)	*M. selenops*
	D. subtilis			(*D. luetkeni*; 100-160)	(*N. valdiviae*; 75)
500	*B. photothorax*	*M. affine*[1]		*D. mollis*	(*N. resplendens*; 75-125)
	H. macrochir	*M. obtusirostre*	75	*C. warmingii*	*L. alatus*
	H. reinhardtii			*D. garmani*	*L. tenuiformis*
	L. ater			*D. termophilus*	*L. luminosa*
	L. luminosa			*D. atlanticus*	*L. gemellarii*
⩾600	*C. warmingii*			*L. guentheri*	
	L. cuprarius		⩾100	*D. effulgens*	*L. ater*
	L. lineatus			*D. fragilis*	*L. cuprarius*
	L. nobilis			*D. rafinesquii*	*L. lineatus*
	T. bathyphilus			*D. subtilis*	
			⩾600	*T. bathyphilus*	

[1]Based on single capture; included because of additional unpublished data.

are separated among these zones as well (Table 6; Fig. 4d). *Diaphus dumerilii* (300 m MDO) and *Notolychnus valdiviae* and *Benthosema suborbitale* (400 m MDO) are upper mesopelagic, while *Myctophum affine* appears to be middle mesopelagic (based also on recent unpublished data of J. V. Gartner). *Ceratoscopelus warmingii* inhabits lower mesopelagic depths during the day, and while both *Lampanyctus alatus* and *Lepidophanes guentheri* have upper mesopelagic MDO's, both are most abundant in the lower mesopelagic zone.

Nighttime patterns show that many species frequently range shallower than their zones of maximum abundance (Table 6) and that all but one species (excluding *Taaningichthys minimus* and *T. paurolychnus*) vertically migrate. Species from four genera (*Myctophum*, 4 spp.; *Hygophum*, 4 spp.; *Centrobranchus nigroocellatus*; *Gonichthys cocco*) are regularly found in the surface waters (0-5 m) at night. However, none of the *Hygophum* species have their highest abundances in this stratum.

Diaphus species show several groupings at night though most occur below 100 m. The *Lampanyctus* species are all most abundant below 75 m, although individuals of *L. nobilis* are taken as shallow as 50 m. *Taaningichthys bathyphilus*, the only *Taaningichthys* species for which we have day and night data characteristically shows no evidence of vertical migration (see also Clarke 1973; Backus et al. 1977). This deep night group also includes nonmigratory individuals of many species.

Of the seven abundant species, four have nighttime MDO's at 75 m which coincide with their zones of maximum abundance (Table 6; Fig. 4d). A fifth species, *N. valdiviae*, while also most abundant below 75 m, occurs as shallow as 50 m. *Benthosema suborbitale* is also captured as shallow as 50 m, but shows no particular zones of abundance at night. *Myctophum affine* is most abundant at the surface.

Vertical partitioning and species associations have also been noted by Karnella (1983). Factorial analysis of abundant species collected from the Bermuda "Ocean Acre" project resulted in from five to eight daytime and six to eight nighttime discrete species associations, depending on season. The Ocean Acre location is in a subtropical region (Backus et al. 1977) and 45 of the 63 species reported by Karnella (1983) also occur in the Gulf. Despite differences in species abundances and general faunal structure and the fact that factorial analysis was inapplicable to the present data set, there are similarities in species associations both day and night between our studies. Karnella (1983) also showed generally shallow daytime distributions for *Diaphus* species, *Lobianchia gemellarii* and *Notolychnus valdiviae* (the only species which is abundant for both studies), and deep (>700 m) daytime distributions for most *Lampanyctus* species and *Ceratoscopelus warmingii*. At night, his surface group included *Myctophum* and *Hygophum* species, *Centrobranchus nigroocellatus*, and *Gonichthys cocco*. Middle groups (30 and 50 m MDO) included *Benthosema suborbitale*, *Ceratoscopelus warmingii*, and *Hygophum* species, while most *Lampanyctus* species were in the deeper (>100 or 200 m, depending on season) groups. The abundant species also tended to be divided among several depth groups both day and night. Our findings are also in general agreement with the distribution and abundance ranges reported by other authors for the same species (Clarke 1973; Badcock and Merrett 1976; Nafpaktitis et al. 1977).

Although vertical stacking of species groups is apparent, it is also obvious that the nighttime overlap of peak abundances among most of the abundant species is quite pronounced (Fig. 4d). It may be that vertical partitioning is on a much finer scale than the present data can resolve or that temporal partitioning of the same depth stratum may occur. It does not seem that day-night MDO's are linked to the extent of vertical migration, since some species which live relatively deep by day (e.g., *Ceratoscopelus warmigii*) are found at the same or shallower depths than those species inhabiting relatively shallow daytime depths (e.g., *Diaphus dumerilii*).

A number of factors including light (e.g., Clarke and Backus 1956, 1964; Paxton 1967; Badcock 1970; Marshall 1980), temperature (Paxton 1967; Robison 1972), and feeding migrations (Marshall 1960) have been suggested as control mechanisms limiting the vertical distribution range of myctophids and other mesopelagic animals. The relationships between these factors and myctophid vertical distributions in the eastern Gulf, however, are not readily apparent. Clarke (1973) determined that lunar period at night was an important factor in limiting the upward extent of vertical migration for many species, finding that the upper depth of migration was depressed by 50 to 125 m during a full moon period for a number of myctophid species (although *Hygophum* species apparently did the opposite, migrating shallower during full moon). In the Gulf, only a single species, *Lepidophanes guentheri*, showed a markedly shallower depth of capture during a new moon period (10 m vs. 75 m during new and full moons, respectively). All other species tended to show the same upper depths of capture regardless of the lunar phase. In fact, individuals of the 10 Gulf species with nighttime surface captures were reg-

ularly taken at the surface under a full moon with the deck lights turned on. The effect of temperature in the eastern Gulf is also unclear since the night distributions of almost all species extend through the base of the thermocline and many species enter the mixed layer which is generally isothermal (Fig. 2). Thus, many species encounter the highest temperatures found in Gulf surface waters.

If, as Marshall (1960) and later researchers suggested, nighttime vertical migrations of myctophids and other midwater animals are feeding migrations, a third possible control of depth range would be prey density. In this case, it would be reasonable to assume that zones of maximum potential prey and predator densities would be closely correlated. Analysis of zooplankton catches taken concurrently with our fish trawls show that this is not the case in the eastern Gulf (see Hopkins 1982). Rather, maximum zooplankton biomass of potential forage size organisms occurs in the upper 30 m at night in the eastern Gulf (Hopkins 1982), which is well above the MDO's of all species except surface dwelling *Myctophum* species, *C. nigroocellatus*, *G. cocco*, and occasional individuals of *Hygophum* species and *L. guentheri*.

Size Structure

The trend of increasing body size or advancing ontogenetic stage with increasing depth has been demonstrated among myctophids by many workers (Badcock 1970; Gibbs et al. 1971; Clarke 1973; Badcock and Merrett 1976; Willis and Pearcy 1980; Hulley 1981; Robison et al.[5]). Our data, which are confined to the abundant Gulf species, are in general agreement with these earlier findings for all species at night and for most during the day as well.

Many myctophid populations have individuals which do not migrate on a daily basis, and these nonmigrators are usually small juveniles (Gibbs et al. 1971; Clarke 1973; Badcock and Merrett 1976; Willis and Pearcy 1980). Our data also show this in that at least 19 of the 49 Gulf species had individuals captured at or below daytime depths (Table 3). In comparison with published accounts of identical species, our data on nonmigratory individuals supports the findings of Clarke (1973) for *Benthosema suborbitale*, *Bolinichthys supralateralis*, *Ceratoscopelus warmingii*, *Lampadena luminosa*, and *Lampanyctus nobilis* off Hawaii, and of Badcock and Merrett (1976) for *B. suborbitale*, *Diaphus rafinesquii*, and *Hygophum reinhardtii* in the eastern North Atlantic. Badcock and Merrett also captured *C. warmingii* but did not observe nonmigration, possibly because they took no individuals of the deep nonmigratory size range. Both Clarke (1973) and Badcock and Merrett (1976) reported that *Notolychnus valdiviae* had a significant nonmigratory fraction of the population, whereas in the Gulf the entire population apparently migrated.

Comparison of the size ranges of our abundant species with published sizes of the same species from other tropical-subtropical areas (Clarke 1973; Hulley 1981) show distinctly smaller sizes of adult individuals in the Gulf (Table 7). With a few exceptions, none of the Gulf species approaches maximum recorded sizes. This may have to do with sampling mechanics (e.g., net mouth area, towing speed, and net avoidance); however, the fact that we have made many additional net hauls since 1977 (20 cruises, ca. 600 discrete depth and oblique samples from 0 to 1,000 m) with a variety of gear and have not significantly increased the upper size limit of the abundant species suggests that this is not the case. A second possibility, which is supported by research on a variety of inshore and offshore species, is that fish species in the Gulf tend to grow faster, with given developmental stages being smaller, and reach maturity at smaller sizes than the same species found outside the Gulf (e.g., *Cynoscion nebulosus*, Tabb 1961; *Micropogonias cromis*, White and Chittenden 1977; *Mycteroperca microlepis*, Manooch and Haimovici 1978; *Mycteroperca phenax*, Godcharles and Bullock 1984; adult *Sciaenops ocellatus*, Mur-

TABLE 7.—Size range comparisons of dominant eastern Gulf myctophid species with the same species from other tropical-subtropical regions.

Species	This study	Clarke (1973) Hawaii	Hulley (1981) Eastern and South Atlantic
Ceratoscopelus warmingii	14-65	11-79	25-80
Notolychnus valdiviae	9-22	9-25	[1]19
Lepidophanes guentheri	13-64		29-76
Lampanyctus alatus	15-48		30-58
Diaphus dumerilii	12-53		25-85
Myctophum affine	12-58		[2]28-47
Benthosema suborbitale	10-30	9-38	20-33

[1]Based on 1 specimen.
[2]Based on 13 specimens.

[5]Robison, B. H., T. L. Hopkins, and J. J. Torres. Ecology, physiology and nutrient energy dynamics of the Southern Ocean myctophid *Electrona antarctica*. Manuscr. in prep. Marine Science Center, University of California at Santa Barbara, Santa Barbara, CA 93106.

phy and Taylor MS in review[6]; larval and juvenile *S. ocellatus*, M. M. Leiby[7]; deep-sea benthic fishes, K. J. Sulak[8]).

Species Composition, Zoogeographic Affinities, Hydrographic Influence

Relatively few accounts have been published on Gulf of Mexico myctophids. Rass (1971) examined material from 5 years of deep otter trawl collections and reported 20 species. Bekker et al. (1975) identified 31 species from 19 stations in the southwestern Gulf, while Backus et al. (1977) collected 38 species from 7 midwater trawl stations extending from the north central to the southwestern Gulf. Nafpaktitis et al. (1977) recorded 52 species based on a variety of collections and earlier accounts from throughout the Gulf. Murdy et al. (1983) listed 39 species of myctophids taken from 35 Isaacs-Kidd Midwater Trawl stations also located throughout the Gulf. Most recently, Hopkins and Lancraft (1984) reported 34 species from 28 oblique hauls taken with an open net between 0 and 1,000 m at Standard Station. With the exception of Backus et al. (1977) and Nafpaktitis et al. (1977), these accounts are mainly annotated species lists.

Of these earlier studies, only Bekker et al. (1975) and Nafpaktitis et al. (1977) reported myctophid species not found in the present study. Bekker et al. captured one specimen each of *Lampadena anomala* and *Lampanyctus festivus*. Nafpaktitis et al. listed five species (*Diaphus adenomus, D. anderseni, D. metopoclampus, D. minax, Lepidophanes gaussi*) from the Gulf which we have not collected. The records of *D. anderseni* and *D. minax*, each based on a single specimen from our University of South Florida collections, were found to be misidentifications of *D. brachycephalus* and *D. perspicillatus*, respectively. Of the other five species, *D. adenomus* appears to be epibenthic (Clarke 1973; Hulley 1981) and as such cannot be considered part of the mesopelagic myctophic assemblage. The captures of *Lampadena anomala, Lampanyctus festivus*, and *D. metopoclampus* were well to the south and west of our study areas. Because of differences in circulation patterns of western and eastern Gulf waters, these species may never occur as far east as our sampling areas. Thus, the only species that we cannot reconcile is *Lepidophanes gaussi*, which was reported from the eastern Gulf by Nafpaktitis et al. (1977), although at best this species appears to be an exceedingly rare visitor.

Despite these records, we feel that with the data from the present study, the eastern Gulf of Mexico myctophid fauna has been defined. Of our 49 species, 42 were taken on the first three cruises and all 49 were collected by 1976. Despite an additional 20 cruises with approximately 600 mesopelagic trawl samples and over 8×10^6 m^3 water filtered, we have not added a single new species. We also conclude that all 49 species, including the 6 species listed as rare, are typical components of the eastern Gulf myctophid assemblage during the warm months. In other studies of myctophid assemblages (Clarke 1973; Karnella 1983), the term "rare" is used to designate species whose centers of geographic distribution lie outside the study area but which may occasionally be captured as strays, a definition which does not apply in the present study. With the exception of *Hygophum hygomii*, whose low numbers are attributed to geographic exclusion by its congener, *H. benoiti* (Nafpaktitis et al. 1977), the rare species in the eastern Gulf are everywhere rare or extremely uncommon. Data from the upper 1,000 m collected in the eastern Gulf since 1977 show all but the *Taaningichthys* species, which may occur below our normal fishing depth ranges, to be persistent low abundance members of the myctophid assemblage. Additional evidence of this is the capture of the larvae of *Symbolophorus rufinus* and *Notoscopelus caudispinosus* in the eastern Gulf (Houde et al. 1979; W. J. Conley[9]).

The number of myctophid species associated with a particular distribution pattern as defined by Backus et al. (1977) are listed in Table 8. Three of the 49 species captured in the Gulf (*Diaphus taaningi, Taaningichthys bathyphilus, T. paurolychnus*) are omitted because they have indeterminate geographic distributions. *Diaphus taaningi* is a pseudooceanic species, associated primarily with land, while the two *Taaningichthys* species are bathypelagic and do not appear to conform to shallower mesopelagic zoogeographic patterns.

Representatives of five of the nine Atlantic distribution patterns established by Backus et al. (1977)

[6]Murphy, M. D., and R. G. Taylor. Reproduction, growth and mortality of red drum, *Sciaenops ocellatus* in Florida. Manuscr. in prep. Department of Natural Resources, Bureau of Marine Research, 100 8th Avenue S.E., St. Petersburg, FL 33701.

[7]M. M. Leiby, Florida Department of Natural Resources, Bureau of Marine Research, 100 8th Avenue S.E., St. Petersburg, FL 33701, pers. commun. January 1986.

[8]K. J. Sulak, Atlantic Reference Centre, Huntsman Marine Laboratory, St. Andrews, New Brunswick E0G 2X0, Canada, pers. commun. June 1986.

[9]W. J. Conley, University of South Florida, Department of Marine Science, 140 7th Avenue S.E., St. Petersburg, FL 33701, pers. commun. September 1985.

TABLE 8.—Distribution patterns of eastern Gulf myctophids. NE - northeast, EC - eastern central, SE - southeastern.

	Total no. of species			No. of species by region (percent total no. of specimens)			Percent total no. of specimens	
	Atlantic (Backus et al. 1977)	Gulf (Backus et al. 1977)	Gulf (This study)	NE	EC	SE	Backus et al. 1977[1]	This study
Temperate-Semisubtropical	8	3	3	2(3.4)	3(4.2)	2(1.5)	0.3	3.9
Subtropical	13	5	7	7(4.0)	6(5.2)	6(6.6)	2.1	5.1
Tropical-Subtropical	18	13	15	11(51.1)	14(40.9)	12(45.4)	64.8	42.4
Tropical-Semisubtropical	5	4	5	5(2.4)	5(4.9)	5(6.2)	1.4	4.6
Tropical	18	12	16	16(37.9)	16(44.6)	13(39.8)	31.0	43.5

[1]Collections from shallower than 200 m at night.

are found in our collections. Species with tropical and tropical-subtropical affinities predictably form the largest component of the Gulf myctophid assemblage during the summer, comprising almost 70% of the 46 species. The seven abundant species all belong to one of these two faunal associations: three (*Ceratoscopelus warmingii*, *Notolychnus valdiviae*, *Benthosema suborbitale*) are tropical-subtropical; the other four (*Lepidophanes guentheri*, *Lampanyctus alatus*, *Diaphus dumerilii*, *Myctophum affine*) are tropical. Species with subtropical and temperate-subtropical affinities, however, are poorly represented in our collections. A comparison of species number by sampling locale (NE, EC, SE) within the Gulf reveals no particular pattern (Table 8). Absences from an area are probably due to species rarity or inadequate depth coverage of samples rather than to geographic influence.

Backus et al. (1977) characterized the mesopelagic Gulf of Mexico as a special zoogeographic region because of its unique physical and faunal characteristics. Although our collections captured a larger number of species than did theirs (49 vs. 38), the species composition patterns are very similar (Table 8) and indicate that the Gulf myctophid assemblage is overwhelmingly dominated by tropical-subtropical species. However, comparison of the percentage contribution of species within the two collections shows a much different composition (Table 8). Where the data of Backus et al. (1977) showed a 2:1 numerical predominance of tropical-subtropical myctophids over tropical species, our findings indicate that the two groups are roughly equal. This discrepancy may be due to the fact that Backus et al.'s data were based on collections from the western Gulf which has a different circulation pattern and is less directly influenced by the tropical Loop Current (Jones 1973). Their data were also from collections <200 m at night (J. E. Craddock[10]) which could have affected species number and percentages.

The largely tropical and tropical-subtropical composition of the eastern Gulf, during the warmer months at least, is most probably due to the influence of the Loop Current, which may entrain individuals of many uncommon species from the Caribbean. The size ranges of some of the species taken in our collections support such a hypothesis for transient species. Among the 26 uncommon species, 15 are represented only by either newly metamorphosed through juvenile or juvenile stages (Table 3). This suggests that the large, sexually mature adults may occur and spawn outside the Gulf, with occasional transport of eggs, larvae, and juveniles into the Gulf via the Loop Current. Four of the 15 species, however, are deep-dwelling *Lampanyctus* (*L. ater*, *L. cuprarius*, *L. nobilis*, *L. tenuiformis*) and the sexually mature individuals of these species may be present in the Gulf below our normal fishing depths, i.e., >1,000 m.

Other evidence of Loop Current influence is the relative absence of subtropical species whose geographic distributions usually place them at higher latitudes well to the north or south of the Caribbean Sea and Florida Straits. This is reinforced by the fact that of the six subtropical species we recorded from the Gulf, four (*Hygophum reinhardtii*, *Lampanyctus ater*, *L. lineatus*, *Taaningichthys minimus*) have uncertain zoogeographic affinities, as they seem to occur often in lower latitudes, including the Caribbean and the Gulf (Backus et al. 1977).

Although the Loop Current appears to play an important role in the composition of the eastern Gulf myctophid fauna, the biomass transported appears to be low. Comparison of the 25 northern (NE) non-

[10]J. E. Craddock, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, pers. commun. August 1978 (reconfirmed July 1986).

Loop Current-influenced stations with the 36 southern (SE) Loop Current samples showed that the samples were comparable in diel and vertical depth coverage and that species composition was also similar. However, the number of specimens collected at the NE sites were almost 2.5 times that of the SE total. This apparent impoverishment of myctophids in Loop Current waters is supported by the data of other workers showing low biomass of zooplankton in the Loop Current (Austin 1971; Jones 1973).

Tropical-Subtropical Myctophid Faunal Structure

The only other work which has extensively analyzed the myctophid assemblage in a tropical-subtropical setting is that of Clarke (1973) in the waters off Hawaii (lat. 21°N, long. 158°W). Estimates of micronekton standing stock off Hawaii (Maynard et al. 1975) and in the eastern Gulf (Hopkins and Lancraft 1984) show that both ecosystems are oligotrophic with roughly equivalent micronekton biomass in the upper 1,000 m. Because of these similarities, a direct comparison between the present study and the findings of Clarke (1973) is possible.

High diversity was apparent in both myctophid assemblages, with 18 genera, 47 species off Hawaii (Clarke 1973) and 17 genera, 49 species in the eastern Gulf. Of these taxa, the two systems shared 21 species. Excluding 2 bathypelagic species and 2 species of uncertain affiliation, 10 species are tropical-subtropical, 5 are tropical and 2 are tropical-semisubtropical according to Backus et al. (1977). Of the seven numerically dominant species of both studies, three (*Benthosema suborbitale*, *Ceratoscopelus warmingii*, *Notolychnus valdiviae*) are shared (Table 9). In fact, *C. warmingii* is the top ranked species on both lists. The other dominants on Clarke's list are Pacific congeners of Atlantic-Caribbean species, or are in very closely related genera (Paxton 1972). The percent of the total number of individuals that the top seven species comprise is strikingly similar (75.5%, Hawaii, 74.7% Gulf). Considering the difference in gear types and sampling strategy, estimates of numbers of individuals for the three shared species also agree well. Clarke's (1973) abundance ranges for *B. suborbitale* during warm months was 14 to 23 $\times$ 10^3 m^2, compared with 32 to 42 in the Gulf; *C. warmingii*; 55 to 155 vs. 86 to 287; *N. valdiviae*; 23 to 104 vs. 27 to 128. Thus, the contribution of the abundant species in the myctophid faunas appears to remain relatively constant.

Clarke's (1973) data on diel distributions of *B. suborbitale*, *C. warmingii*, and *N. valdiviae* are also similar to our own. Some differences, which may be the result of localized environmental variations, include shallower MDO's, depression of MDO and zones of abundance during full moon and roughly equivalent day-night abundances off Hawaii. Additionally, members of the Hawaiian *N. valdiviae* population were found to have a significant nonmigratory fraction, which has not been observed in the Gulf population. Clarke (1973) did note, however, that during several collection periods (March and June) no evidence of nonmigration was observed in *Notolychnus*.

Comparison of our species list with those compiled from other studies encompassing tropical-subtropical latitudes (Nafpaktitis and Nafpaktitis 1969, Indian Ocean; Hulley 1972, SW Indian Ocean; Clarke 1973, central Pacific; Wisner 1976, eastern Pacific; Hulley 1981, eastern and South Atlantic) showed that 10 myctophid species (8 mesopelagic, 2 bathypelagic) were common to all regions and that three (*Benthosema suborbitale*, *Ceratoscopelus war-*

TABLE 9.—Comparison of the top seven myctophid species and their percentage composition for the tropical-subtropical community off Hawaii (from Clarke, 1973) and the eastern Gulf of Mexico (the present study). Underline indicates shared species.

Hawaii			Eastern Gulf of Mexico		
Species	No.	Percent of total specimens	Species	No.	Percent of total specimens
Ceratoscopelus warmingii	3,911	20.7	*Ceratoscopelus warmingii*	2,267	17.0
Lampanyctus steinbecki	2,362	12.5	*Notolychnus valdiviae*	1,780	13.4
Triphoturus nigrescens	2,120	11.2	*Lepidophanes guentheri*	1,610	12.1
Lampanyctus niger	1,946	10.3	*Lampanyctus alatus*	1,418	10.7
Bolinichthys longipes	1,458	7.7	*Diaphus dumerilii*	1,279	9.6
Notolychnus valdiviae	1,267	7.0	*Myctophum affine*	893	6.7
Benthosema suborbitale	1,157	6.1	*Benthosema suborbitale*	687	5.2
	Total	75.5		Total	74.7

mingii, *Notolychnus valdiviae*) were relatively abundant everywhere. Distributional affinities of six of the eight mesopelagic species (the three preceding species plus *Diogenichthys atlanticus*, *Lampadena luminosa*, and *Myctophum nitidulum*) are tropical-subtropical; the other two (*Lampanyctus nobilis* and *L. tenuiformis*) are tropical (Backus et al. 1977). These species represent 5% to 17% of the total number of species from each region and between 9% and 38% of the total number of specimens examined (Wisner 1976 excluded). Thus, based on our comparison with Clarke's (1973) Hawaiian myctophid assemblage and the species lists from various regions of the world ocean, our findings on the eastern Gulf of Mexico myctophid fauna provide additional support to the idea that oligotrophic low-latitude mesopelagic habitats show considerable structural and ecological uniformity allowing for circumglobal distribution of a number of species, a pattern similar to that demonstrated to an even greater degree by bathypelagic fish species (Marshall 1980).

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LIFE HISTORY AND FISHERY OF THE CALIFORNIA SCORPIONFISH, *SCORPAENA GUTTATA*, WITHIN THE SOUTHERN CALIFORNIA BIGHT

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ABSTRACT

We examined the life history of the California scorpionfish in the Southern California Bight. Based on sportfish creel census data, the species was most abundant in the southern part of the Bight, particularly around Catalina, San Clemente, and the Coronado Islands. Trawl studies from 1974 to 1984 indicated that California scorpionfish populations varied considerably in abundance, with numbers peaking in 1982. Though the species usually associates with hard substrata, it was abundant over mud about the Palos Verdes Peninsula, site of a major sewage outfall. We think that this anomalous abundance was due to the presence of large numbers of a prey species, the ridgeback prawn, *Sicyonia ingentis*, which was attracted to the nutrient-rich substrata.

Female California scorpionfish lived to 21 years, males to 15. Females grew faster than males. Von Bertalanffy age-length parameters for females were $L = 44.3$, $k = 0.13$, $t_0 = -1.9$, and for males $L = 36.3$, $k = 0.12$, $t_0 = -3.86$. Over 50% of both females and males were mature at 2 years of age. Males tended to mature at a slightly smaller size. Spawning occurred from May through August, peaking in July. California scorpionfish formed large offshore spawning aggregations in waters deeper than their off-season habitat. Tagging results indicated that fish return to the same spawning area annually. Crabs, primarily juvenile *Cancer anthonyi*, were the most important food item of fishes inhabiting soft substrata in shallow water.

The family Scorpaenidae is represented by four genera in the northeastern Pacific—*Scorpaena*, *Scorpaenodes*, *Sebastes*, and *Sebastolobus* (Eschmeyer et al. 1983). One *Scorpaena* species, *S. guttata*, the California scorpionfish, is abundant as far north as southern California.

The California scorpionfish is a medium-sized [to 43 cm TL (total length)], generally benthic species, found from central California into the Gulf of California between the intertidal and 183 m (Eschmeyer et al. 1983). It occurs on rocky reefs (often lodged in crevices), although in certain areas and seasons it aggregates over sandy or muddy substrata (Frey 1971; present paper). This species is oviparous, producing floating, gelatinous egg masses in which the eggs are embedded in a single layer (Orton 1955). Like others in the genus *Scorpaena*, California scorpionfish produce a toxin in their dorsal, anal, and pelvic spines, which produces intense, painful wounds. California scorpionfish comprise a minor part of the California sport and commercial fisheries (Wine and Hoban[3], Wine[4], Knaggs[5], present paper).

Perhaps because of this relatively small catch, the species has not been the subject of an in-depth life history study. Rather, much of what is known has been gleaned from larger ecological surveys (Table 1), in which the species played a minor role. However, California scorpionfish have recently become important in pollution-related studies (Table 1), deriving from 1) its abundance about the Palos Verdes Peninsula (heavily polluted from the Whites Point sewage outfall which services Los Angeles), 2) its ease of capture by otter trawl and by hook and line, and 3) its ability to adapt to laboratory aquaria.

This increased interest has given rise to questions regarding the species' growth rate, age at first maturity, and movements. Our paper details some

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[3]Wine, V., and T. Hoban. 1976. Southern California independent sportfishing survey annual report, July 1, 1975–June 30, 1976 Calif. Dep. Fish Game, 109 p.
[4]Wine, V. 1979. Southern California independent sportfishing survey annual report, July 1, 1977–June 30, 1978. Calif. Dep. Fish Game, 100 p.
[5]E. Knaggs, California Department of Fish and Game, Long Beach, CA, pers. commun. May 1985.

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TABLE 1.—Previous studies involving *Scorpaena guttata*. Not included are geographical species lists.

Systematics.—Girard 1854, 1858; David 1943; Phillips 1957; Tsuyuki et al. 1968; Eschmeyer and Bailey 1970; Greenfield 1974.
Anatomy and Physiology.—Clothier 1950; Halstead 1951; Halstead et al. 1955; Saunders 1959; Halstead and Mitchell 1963; Taylor 1963; Munz 1964; Russell 1965, 1969; Carlson et al. 1971; Schaeffer et al. 1971; Baines 1975; Sullivan and Somero 1980.
Pollutant Levels and Effects.—MacGregor 1972; Young and Mearns 1978; Stout and Beezhold 1981; Brown et al. 1982, 1984a-c; Gossett et al. 1982a, b, 1984; Jenkins et al. 1982; Mearns 1982; Schafer et al. 1982; Szalay 1982; Gadbois and Maney 1983; Bay et al. 1984a, b; Perkins and Rosenthal 1984; Rosenthal et al. 1984; Cross et al. 1985.
Life History, Distribution, and Behavior.—Jordan and Gilbert 1881; Holder 1900; Richardson 1905; Wilson 1908, 1935; Barnhart 1932; David 1939; Limbaugh 1955; Orton 1955; Montgomery 1957; Causey 1960; Kunnenkeri and Martin 1963; Rosenblatt 1963; Taylor 1963; Arai and Koski 1964; Carlisle et al. 1964; Clarke et al. 1967; Quast 1968a-c; Carlisle 1969; Cressey 1969; Taylor and Chen 1969; Turner et al. 1969; Frey 1971; Hobson 1971; Ho 1972; Miller and Lea 1972; Varoujean 1972; Feder et al. 1974; Allen et al. 1976; Burreson 1977; Mearns 1979; Dailey et al. 1981; Helvey and Dorn 1981; Hobson et al. 1981; Stephens and Zerba 1981; Eschmeyer et al. 1983; Love and Moser 1983; Barnett et al. 1984; DeMartini and Allen 1984; Larson and DeMartini 1984; Thresher 1984; Love and Westphal 1985.
Fishery.—Phillips 1937; Daugherty 1949; Roedel 1953; Frey 1971.

aspects of the growth, reproduction, food habits, movements, and fisheries of the California scorpionfish.

METHODS

Distribution and Movements of Adults and Juveniles

To estimate relative abundance of California scorpionfish over reefs and hard substrata, we used the California Department of Fish and Game creel census data, gathered from throughout the Southern California Bight from April 1975 to December 1978. In this study, Fish and Game personnel rode aboard randomly chosen commercial passenger vessels (hereafter referred to as "partyboats") and measured and identified all fish captured. The sampler also noted numbers of anglers, fishing hours, and location and depth of each fished site. Catch per unit effort was used as our estimate of relative abundance, where effort was measured in angler hours (number of anglers × number of hours fished).

For several reasons, data from this study could not give a completely unbiased estimate of California scorpionfish abundance. First, virtually all fishing effort aboard partyboats occurs over reefs and hard substrata. Hence, this data base does not effectively measure abundance over soft substrata. Second, most angling involved fishing with live bait (primarily northern anchovies, *Engraulis mordax*) or with lures simulating fishes. Thus the sample was biased away from very small individuals. However, California scorpionfish develop relatively large mouths and become mesocarnivores at relatively early sizes and our data indicates that most size classes were represented. As angling techniques were similar throughout the Southern California Bight, we believe this survey allows for an acceptable representation of abundance of all but the smallest size classes.

To measure relative abundance of California scorpionfish living on soft substrates, we used trawl data collected by the Southern California Coastal Water Research Project (SCCWRP) and the Orange County Sanitation District. These data were based on 10-min tows of a 7.6 m headrope otter trawl fished on the bottom at about 23, 61, and 137 m off Palos Verdes and Huntington Beach (trawling stations are illustrated in Cross [1985] and Orange County Sanitation District[6]). We analyzed data taken about Palos Verdes and Huntington Beach from January 1974 to December 1984 (except that no data was taken for Huntington Beach during 1975). Fishes in this survey were measured using standard length. We converted these measurements to total lengths using conversion factors based on measurements of 1,083 California scorpionfish. These factors are TL = (1.21)SL + 1.02; SL = (0.82)TL − 0.69.

We also conducted a tagging program to give some insight into this species' movements. We tagged trawl-caught California scorpionfish with Floy[7] tags (orange FD-68BC) from an area between the southern part of Santa Monica Bay and Huntington Beach. The tags (consisting of a plastic tube 50 mm long with a 10 mm cross bar) were injected into the dorsal musculature between the second and third dorsal spines, leaving the brightly colored end free. Most of the tagging effort was centered on Dago Bank, about 11 km southeast of Long Beach Harbor—an area we had identified as a spawning ground. A monthly otter trawl survey indicated that California scorpionfish were rare in this area between October and April, with large numbers of ripe individuals occupying the habitat during late spring and summer.

[6]Orange County Sanitation District. 1984. Annual Report, 300 p.

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Juveniles and Adults Collection

Individuals used in the analysis of age and length, length-weight, and reproduction were sampled monthly (2-10 samples/month) from May 1981 to June 1982 (and sporadically thereafter through May 1983). We used a 7.6 m (25 ft) or 4.9 m (16 ft) headrope otter trawl in 7-90 m of water, between Ventura and San Onofre, CA. All specimens were frozen for later dissection. After thawing, all fish were measured (total length and standard length), weighed, and sexed, and the gonads were removed and weighed.

Fish for food habit studies were taken by otter trawl over soft substrata in 6-16 m of water between Santa Monica Bay and San Onofre. These samples were frozen immediately after collection. In the laboratory, food items were identified to lowest possible taxa, then weighed and counted.

Techniques for Aging Juveniles and Adults

We attempted to age California scorpionfish by a variety of calcified structures (sagittae, scales, vertebrae, and pterygiophores) and found that cross sections of anal pterygiophores gave best results. The fused first and second anal pterygiophores (supporting the first and second anal spines) were removed from 613 specimens, cleaned, and stored in paper coin envelopes. Pterygiophores were placed on wood blocks and embedded in clear epoxy (Ciba 825 hardener and Ciba 6010 resin). Each block with its pterygiophore was placed on a Buehler Isomet low speed saw and an 0.05 cm wafer was cut through it, using two diamond-edge blades separated by a stainless steel shim. The cut was made near the pterygiophore's site of articulation with an anal spine. Wafers were read under a compound microscope at a magnification of 100×, with both reflected and transmitted light. All wafers were read twice, by M. S. Love, approximately 6 mo apart. When readings did not agree, they were read again. The value of two coincident readings was accepted as the best estimate of age.

We compared the age-length curves of males and females using an analysis of variance of regression coefficients over groups, testing the slopes of the two curves (Dixon 1981). Parenthetically, this was the same test used in comparing male and female length-weight curves. Back calculations of length on age were made using the techniques of Chen (1971).

Procedures for Determining the Timing of Maturation and Reproduction

We estimated length at first maturity by classifying gonads as immature or matured based on the techniques of Bagenal and Braum (1971). Smaller mature fish and fish just entering their first reproductive season become reproductive later in the year. Hence we estimated length at first maturity from just before spawning season (March) through its conclusion (August). A gonadosomatic index [(gonad weight)/(total body weight) × 100] was computed from frozen specimens to quantify changes in gonad size with season.

We computed condition factor $\left(100 \times \frac{(W - GW)}{L^3}\right.$, where W = body weight in grams, GW = gonad weight in grams, and L = total length in centimeters), of mature California scorpionfish. Condition factor was computed using body weight with gonad weight subtracted so as to minimize the effects of seasonal changes in gonad size. We compared these values between seasons within sexes and between sexes, using the Mann-Whitney U-Test (Sokal and Rohlf 1969).

Fishery

To describe the California scorpionfish's role in the commercial passenger vessel (partyboat) sport fishery, we used the previously discussed California Department of Fish and Game creel census data. We also examined the commercial fishery, interviewing fishermen and utilizing the fish landing data of the California Department of Fish and Game.

RESULTS AND DISCUSSION

Distribution and Movements

Data from the Fish and Game creel census indicated differences in abundance between the northern and southern part of the Southern California Bight (Fig. 1). Catch rates were lowest near the city of Santa Barbara and generally increased to the south. Highest catch rates occurred off San Diego and around Catalina, San Clemente, and the Coronado Islands.

Utilizing the same data base, we examined California scorpionfish depth distribution (Fig. 2). Overall, California scorpionfish were taken from barely subtidal waters to 170 m. Depth distribution changed with season. We plotted catch per unit effort in 6

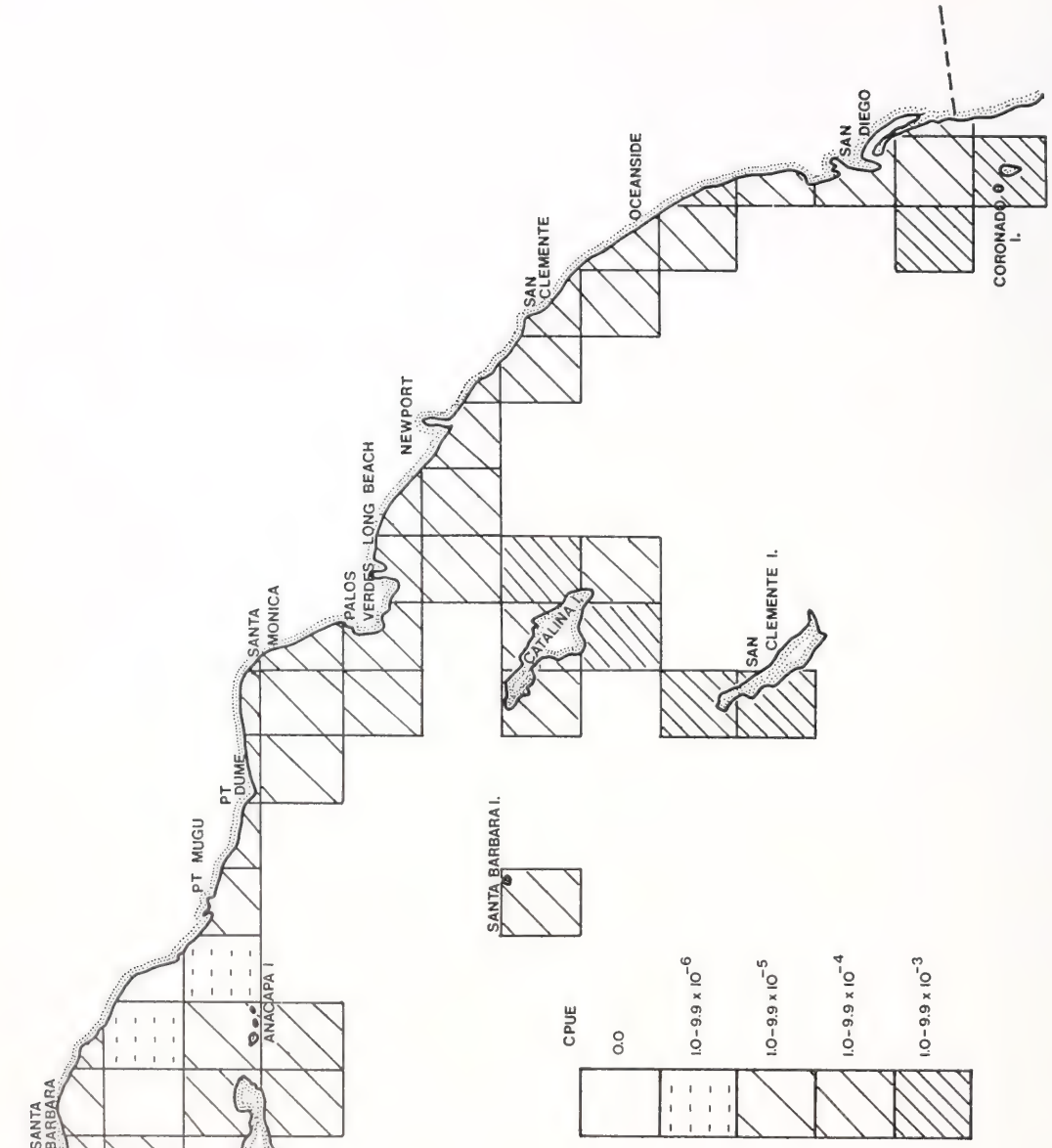

FIGURE 1.—Relative abundances (based on catch per unit effort, fish per angler-hour, in the partyboat sport fishery) of California scorpionfish taken from 1975 to 1978 in the Southern California Bight.

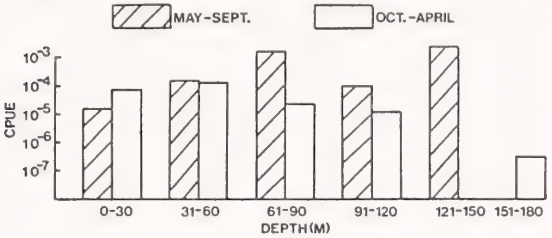

FIGURE 2.—Abundances (based on catch per unit effort in the partyboat sport fishery) of California scorpionfish taken in six depth intervals in the Southern Calfiornia Bight.

depth intervals for two seasons—spawning (May-September) and nonspawning (October-April). During spawning season, fish were most abundant in 61-90 and 121-150 m. Later in the year, there was some inshore movement, and fish were most abundant in 0-30 and 31-60 m. However, it was evident that not all scorpionfish migrate to deeper water at the same time during spawning season. Though catches during May-September were highest in deeper water, there were always some mature individuals inshore. Based on our capturing ripe fishes inshore, it is likely that some spawning occurs there.

Between 29 April 1983 and 24 September 1984, we tagged 518 California scorpionfish and 23 (4.2%) were recovered. The longest time a fish was at liberty was 916 d. Though we tagged fish from a variety of sites, most tagging occurred over Dago Bank. The results of our tagging program indicated that many scorpionfish annually return to the same spawning grounds. Of the 17 tag recoveries made on the Dago Bank, all were fish tagged on the same grounds the previous year. The Dago Bank aggregation site is occupied by scorpionfish during late spring and summer. Catches as high as 800 scorpionfish/20-min tow of a 7.6 m otter trawl occur during spawning season. As few scorpionfish live on Dago Bank during the off season, we believe these tag recoveries indicate that the fish return annually to the same area to spawn. The rest of the returns from fish tagged at their spawning grounds were taken inshore during fall and winter, from sites ranging from El Segundo on the north to Long Beach to the south (Fig. 3). The El Segundo individual had travelled at least 42 km from the spawning grounds.

Based on the SCCWRP and Orange County Sanitation trawl data, California scorpionfish exhibited considerable variation in abundance between 1974 and 1984 (Fig. 4). In the mid-1970's, populations at both sites were relatively low, then increased to a 1982 peak and declined rapidly in 1983 and 1984. An analysis of scorpionfish size frequencies indicates this influx was due to an increase in number of mature fishes. The 1983-84 decline was associated with the El Niño event.

Certainly a number of fish species moved out of their usual haunts during this period (Love et al. 1986). However, if this is correct, it is not clear

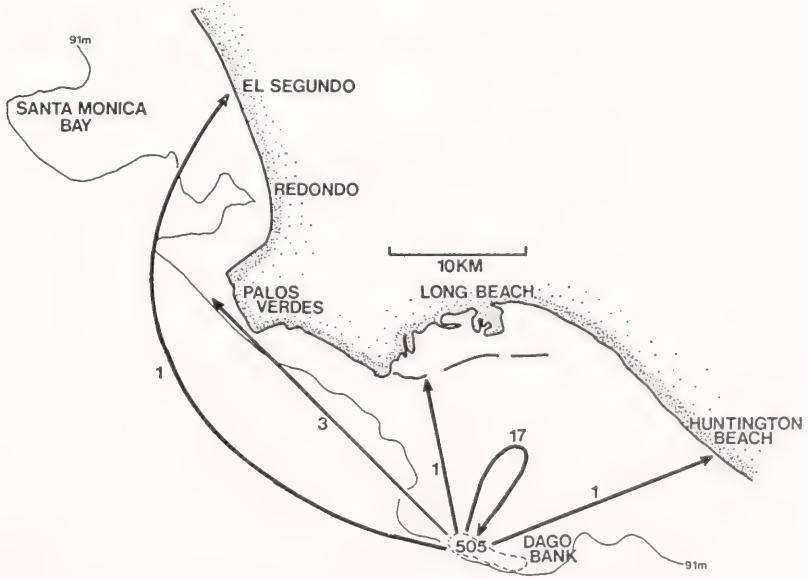

FIGURE 3.—Location of California scorpionfish tagging and return sites.

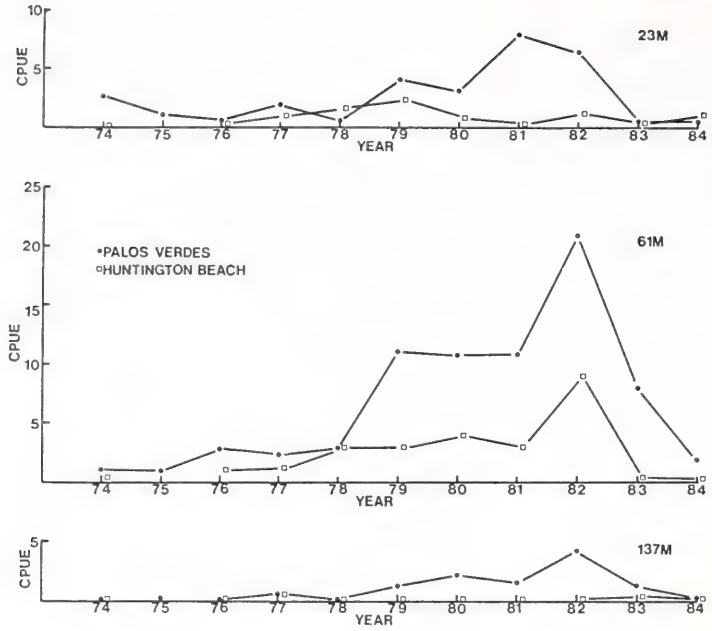

FIGURE 4.—Abundances of California scorpionfish taken by trawl off the Palos Verdes Peninsula and Huntington Beach at three depths from 1974 to 1984.

where the fish went. They did not migrate to deeper waters, as catches did not increase at the deeper stations. It is possible the fish moved north, as we observed a slight increase in commercial trawl-caught scorpionfish off Santa Barbara, 190 km to the north. The populations of several other species (notably bocaccio, *Sebastes paucispinis*; chilipepper, *S. goodei*; and California halibut, *Paralichthys californicus*) seemed to shift northward during the same period.

The presence of California scorpionfish over the soft substrata about Palos Verdes (Fig. 4) attests to the habitat plasticity of this species. This abundance is unusual. For example, the species is only occasionally found over soft substrata to the immediate south (Huntington Beach). We believe the abundance of California scorpionfish over soft substrata about Palos Verdes is linked to the large populations of the ridgeback prawn, *Sicyonia ingentis*, and untimately to the presence of the Whites Point sewer outfall. Both we and Cross[8] have noted that scorpionfish routinely regurgitate these prawns when captured from waters around Palos Verdes.

Studies of sediments about the Santa Monica Bay, Palos Verdes, and Huntington Beach outfalls reveal that substrate deposition of organic material is much greater at Palos Verdes than at the other two sites. This is apparently due to faster water movement and hence greater sewage dispersal at the Santa Monica and Huntington Beach sites (Cross et al. 1985; Cross fn. 8). The large quantities of organics in the Palos Verdes sediment support large populations of ridgeback prawns, populations nearly absent from the other two sites. Additional evidence for this contention comes from the creel census data in Figure 1. These data are based on catches over hard bottom reefs, where ridgeback prawns are not abundant. In this study, California scorpionfish were not more abundant at Palos Verdes than at Santa Monica Bay (to the north) or Huntington Beach (to the south), which have similar environmental parameters. Thus the attraction of the soft substrata around Palos Verdes for scorpionfish is likely to be the one factor which is quite different among the sites—the presence of ridgeback prawns.

Age and Growth

Prior to this study, there was no published work on aging California scorpionfish, the use of pterygiophore sections in age studies had not been validated. To determine if the opaque and translucent zones (as observed by reflected light) were annular,

[8]J. Cross, Southern California Coastal Water Research Project, Long Beach, CA, pers. commun. May 1985.

we observed the development of the opaque zone on the sections' edges in fishes with 2-5 opaque zones. Opaque zone deposition was seasonal, from late winter through summer (Table 2). A relatively large number of pterygiophores (208 = 34%) were not readable because of malformed or poorly delineated annuli. One hundred and eighty-two females (ages 1-21 yr) and 222 males (ages 1-15 yr) were aged.

TABLE 2.—Monthly percentages of 2-5 yr old California scorpionfish with opaque margins.

Month	% opaque	Month	% opaque
January	2	July	89
February	6	August	96
March	28	September	42
April	72	October	16
May	93	November	3
June	92	December	7

Lengths at ages were estimated by direct observation of pterygiophore annuli, back calculated ages, and the von Bertalanffy growth curve model (Tomlinson and Abramson 1961).

$$L_t = L_\infty [1 - \exp - k(t - t_0)]$$

where L_t = length at time t.
L_∞ = theoretical maximum length
k = constant expressing the rate of approach to L_∞
t_0 = theoretical age at which $L_t = 0$

was fitted to the direct observation age-length data.

Since females grew significantly faster than males (ANOVA, $F = 12.5$, $P < 0.001$) and reach a greater size (Fig. 5), we have separated growth data by sex (Table 3).

Mean lengths at ages from direct observations of annuli and those generated by the von Bertalanffy equations are plotted in Figure 5. The oldest female we observed was 21 yr old, the oldest male 15. We have few samples of fish older than 11 yr, and back-calculated lengths (Tables 4, 5) are computed to this age.

TABLE 3.—Parameters of the von Bertalanffy equation for California scorpionfish off Southern California.

Sex	L_∞	SE	k	SE	t_0	SE
Female	44.33	1.57	0.13	0.02	−1.90	0.42
Male	36.31	1.60	0.12	0.02	−3.86	0.68

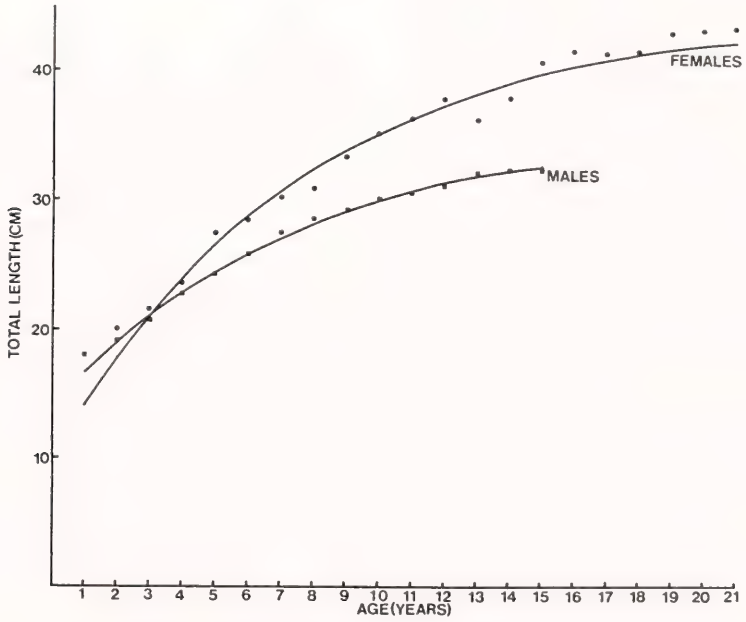

FIGURE 5.—Von Bertalanffy growth curves of female and male California scorpionfish. Also included are mean lengths at age computed from direct observation of pterygiophore annuli. Based on 183 females and 222 males taken in the Southern California Bight, 1981-83.

TABLE 4.—Mean back-calculated total length (centimeters) ±95% confidence intervals at successive annuli for male California scorpionfish captured off southern California, 1981-83.

Age group	No. of fish	1	2	3	4	5	6	7	8	9	10	11
2	7	18.1±1.6	20.4±0.9									
3	31	17.3±0.8	19.5±0.6	21.2±0.6								
4	62	17.2±0.7	19.8±0.7	21.4±0.7	22.5±0.7							
5	40	18.3±0.9	20.7±0.8	22.6±0.8	23.9±0.7	24.9±0.7						
6	15	16.8±1.2	19.9±1.2	21.7±1.0	22.8±0.9	24.0±0.8	25.0±0.6					
7	4	18.2±1.5	20.3±1.6	21.9±1.3	24.0±1.4	25.7±1.7	26.9±1.5	27.6±1.3				
8	9	20.6±1.4	22.7±1.3	24.0±1.8	25.2±1.7	26.5±1.7	27.6±1.5	28.3±1.5	29.2±1.5			
9	5	21.0±2.6	22.9±2.4	23.9±2.3	25.2±1.8	26.0±1.8	27.0±1.5	27.9±1.4	28.5±1.4	29.3±1.5		
10	7	19.7±2.2	21.2±1.8	22.9±2.0	24.2±1.8	25.2±1.5	26.0±1.5	27.0±1.5	28.0±1.5	28.8±1.3	29.4±1.3	
11	4	18.5±1.8	20.6±1.7	22.7±1.1	24.2±1.1	25.0±1.4	26.5±1.3	27.2±1.2	27.8±1.3	29.1±0.4	29.8±0.6	30.5±0.6
Average		17.8	20.2	22.0	23.3	24.5	26.0	27.7	28.4	29.1	29.5	30.6

TABLE 5.—Mean back-calculated total length (centimeters) ±95% confidence intervals at successive annuli for female California scorpionfish captured off southern California, 1981-83.

Age group	No. of fish	1	2	3	4	5	6	7	8	9	10	11
2	3	17.5±0.8	20.6±1.2									
3	31	17.3±0.7	20.2±0.7	22.5±0.7								
4	43	17.7±0.6	20.5±0.7	22.8±0.8	24.2±0.8							
5	31	19.0±1.0	21.8±1.0	24.0±1.1	25.7±1.2	26.8±1.3						
6	24	19.1±1.1	22.0±1.0	24.5±1.0	26.2±1.0	27.7±0.9	28.7±1.0					
7	11	19.1±1.6	21.8±1.8	23.9±1.8	25.5±1.6	26.9±1.6	28.2±1.6	29.4±1.6				
8	3	15.1±4.2	21.0±2.0	23.0±2.8	24.6±2.1	25.8±1.5	27.6±0.8	28.9±0.2	29.7±0.1			
9	1	14.9	23.4	26.5	28.7	30.8	32.4	32.9	34.0	34.5		
10	2	20.8±5.0	24.8±0.7	26.4±0.3	28.0±1.1	30.3±1.6	31.2±2.1	32.6±3.0	33.1±3.0	33.9±2.7	35.1±2.4	
11	1	21.8	26.6	29.5	32.0	33.4	34.4	34.9	35.5	36.3	36.8	37.3
Average		18.2	21.2	23.3	25.3	27.5	28.9	30.4	31.9	34.5	35.4	37.3

All three methods of assessing age and growth (direct observations, back calculations, and von Bertalanffy estimates) yielded roughly similar results, though the method using back-calculated lengths tended to yield faster growth rates than the other two measures, at least for the smaller size classes. Mean lengths at age for females and males were similar through about age 2. Females outgrew males beginning at age 3, when about all males and approximately 60% of females were mature. The maximum theoretical length for California scorpionfish is 44.3 cm (Table 3), close to the maximum observed length of 43 cm (Eschmeyer et al. 1983).

Length-Weight Relationships

A total of 656 males and 371 females from southern California were weighed and measured. The relationship between total length and weight fit the relationship $W = aL^b$, where W = weight in grams, L = total length in centimeters, and a and b are constants, with values determined using $\log_{10}$ transformation and fitting the values to a straight line by least squares (Figs. 6, 7). Males tended to be heavier at a given length (ANOVA, $F = 14.35$, $P < 0.001$). To test whether this difference was an artifact caused by seasonal and gender-related factors, we subtracted gonad weight from body weight, generated the length-weight relationship for each sex, and tested these between sexes. Again, differences between sexes existed (ANOVA, $F = 15.68$, $P < 0.001$).

Condition Factor

Both male and female California scorpionfish displayed differences in condition factor between spawning and resting seasons (Table 6). In both sexes, fish were less robust during the spawning season, perhaps because energy normally utilized for somatic maintenance and growth was shifted to egg and sperm production and spawning behavior. Male California scorpionfish were more robust than females during all seasons.

Maturation and Reproduction

Although a few fish of both sexes matured at 1 yr (14-16 cm TL), over 50% of the males were mature by 17 cm TL and over 50% of the females

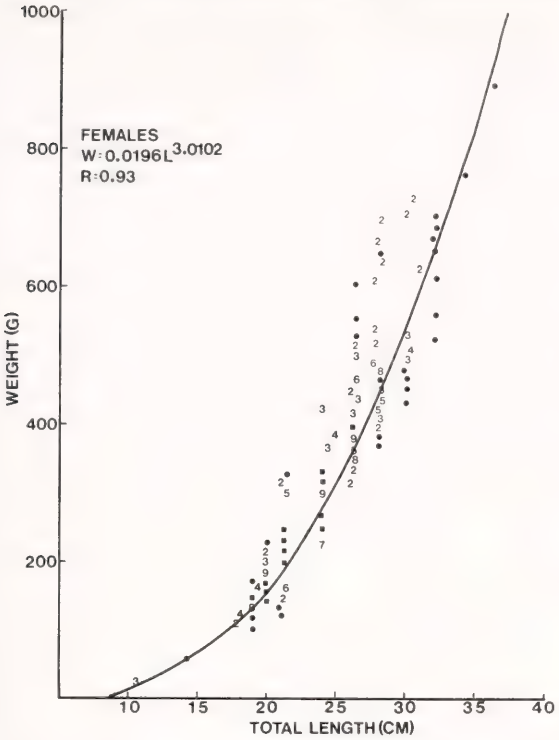

FIGURE 6.—Length-weight relationship of female California scorpionfish sampled in the Southern California Bight, 1981-83. Squares represent more than 10 individuals, dots represent a single fish.

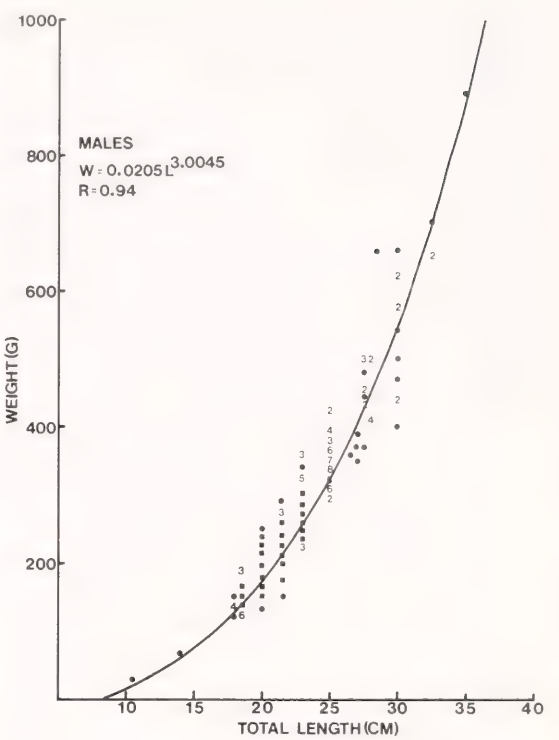

FIGURE 7.—Length-weight relationship of male California scorpionfish sampled in the Southern California Bight, 1981-83. Squares represent more than 10 individuals, dots represent a single fish.

TABLE 6.—Condition factor (K) of California scorpionfish from southern California, 1981-83.

	N	K	SD	U	P
Males					
May-Sept.	398	2.16	0.25	27,729.5	<0.001
Oct.-Apr.	256	1.98	0.18		
Females					
May-Sept.	216	2.07	0.28	13,375.5	<0.001
Oct.-Apr.	180	1.93	0.19		
Sexes combined					
May-Sept.	614	2.13	0.26	104,117.5	<0.001
Oct.-Apr.	436	1.96	0.19		
All seasons					
Males	654	2.09	0.24	79,709.0	<0.001
Females	396	2.00	0.25		

by about 18 cm TL, equivalent to 2 yr of age (Fig. 8). Males tended to mature at a slightly smaller size, though all fish were mature by 22 cm TL.

California scorpionfish spawned from May through August, peaking in July. Ovary and testes sizes varied seasonally (Fig. 9). Ovaries were relatively small and constant in size from September to March but began to increase in April and peaked in June and July, dropping precipitously thereafter (Fig. 9). During the peak spawning season, ovaries comprised about 5% of total weight (maximum 17.5%, minimum 1.0%), while during the transition period, ovaries made up slightly <1% (maximum 1.4%, minimum 0.06%).

Testes followed a similar pattern (Fig. 9). They made up slightly more than 0.3% of body weight during late spring and early summer (maximum 0.6%, minimum 0.2%) declining to 0.1% in winter (maximum 0.3%, minimum 0.05%).

We believe spawning takes place just before, and perhaps after dawn, in the water column. On several occasions, about 1 h before sunrise, while conducting surveys on the California scorpionfish spawning grounds, we observed dozens of scorpionfish near the surface. Fathometer tracings indicated large numbers of fish throughout the water column. These fish disappeared just after sunrise. Commercial longline fishermen, targeting scorpionfish on the same grounds, report this is a daily phenomenon. There is no evidence that California scorpionfish behave in this fashion when not in spawning condition.

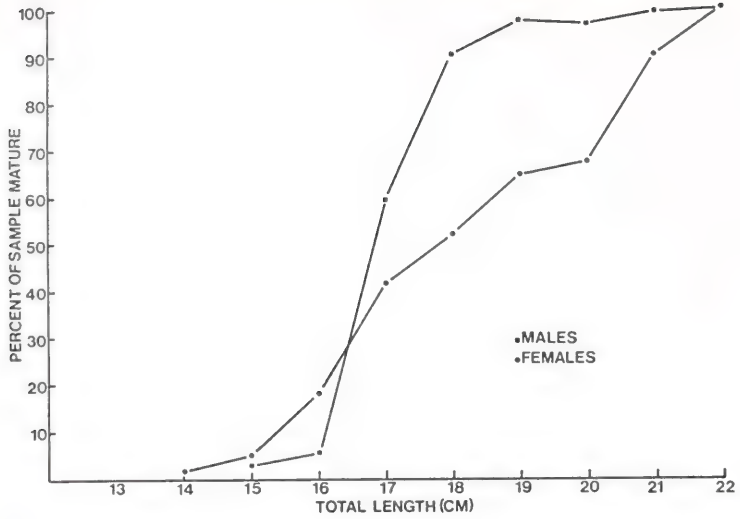

FIGURE 8.—Length-maturity relationship in 246 female and 223 male California scorpionfish collected in the Southern California Bight, 1981-83.

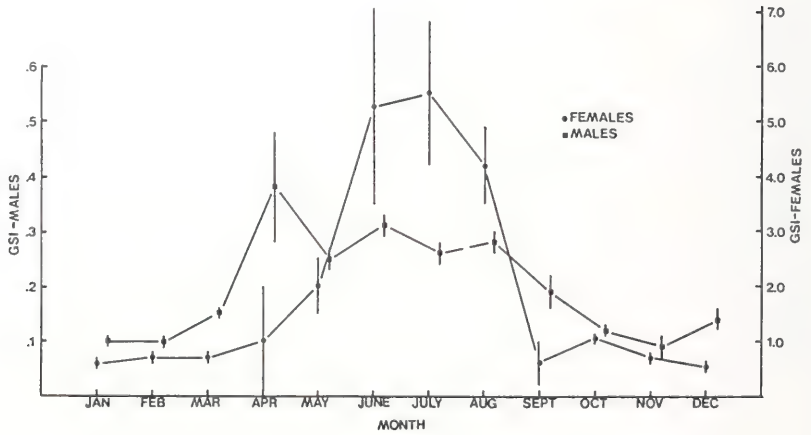

FIGURE 9.—Seasonal changes in the gonosomatic indices (GSI = gonad weight as a percentage of total body weight) of female and male California scorpionfish (based on 396 females and 654 males). Vertical lines indicate 95% confidence intervals of the mean.

We know little of the location of California scorpionfish larvae in the Southern California Bight. Over the past 30+ yr, few have been taken in offshore waters despite considerable numbers of ichthyoplankton surveys (Moser[9]). Moreover, only a few are known from ichthyoplankton surveys conducted in inshore waters (Barnett et al. 1984; McGowan[10]). Particularly puzzling is the lack of larvae taken in King Harbor, Redondo Beach. No larvae were caught during a 7-yr monthly survey, of both surface and bottom waters (Jordan[11]) despite the abundance of young-of-the-year and 1-yr-old fish in the Harbor.

It appears that California scorpionfish utilize an "explosive breeding assemblage" reproductive mode

[9]G. Moser, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. September 1985.

[10]G. McGowan, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, pers. commun. May 1985.

[11]G. Jordan, VANTUNA Research Group, Occidental College, 1600 Campus Road, Los Angeles, CA 90041, pers. commun. May 1985.

(Emlen and Oring 1977), in which fish migrate to, and aggregate at a "traditional" spawning site for brief (though undefined) periods. Reproduction is polygamous and sexual selection is low. Thresher (1984) speculated such behavior may be the primary reproductive mode of larger pelagic spawning reef fishes—such as snappers, jacks, and barracudas. Smaller fishes would find a spawning migration deleterious, owing to a higher predation risk while traveling.

California scorpionfish do indeed migrate to "traditional" spawning areas and are pelagic spawners. With 50% maturing at 17 cm, they are smaller than the usual explosive breeding assemblage species listed by Thresher (1984). However, it is likely that mature California scorpionfish are not heavily preyed upon (because of their toxin-carrying spines) and thus may be an exception to the rule.

The Dago Bank spawning site is, for the most part, a sandy environment, usually inhabited by relatively few fish. Spawning in a deep-water, relatively depauperate area, the California scorpionfish may avoid some of the egg predation expected in the shallow reefs inhabited during fall-spring. Moreover, by spawning well above the substrata, newly spawned eggs are kept away from benthos-dwelling predators. Many coral reef fishes exhibit the same behavior, which not only decreases egg predation but also places the fertilized eggs into surface currents, increasing the chances of larval dispersal (Thresher 1984).

We do not know how many spawning sites exist off southern California. Santa Monica Bay (Turner et al. 1969) and Dana Point (Cross fn. 6) are likely sites while Anacapa Island and the Coronado Islands (M. Love, unpubl. data) might also be utilized. We have no data on how many years these sites persist as spawning areas. Judging from other species (such as *Clupea harengus*—Cushing 1982), it is likely that scorpionfish spawning grounds are probably of long duration.

For several reasons, this behavior is unusual among fishes in southern California. First, only a few species (notably kelp bass, *Paralabrax clathratus*; barred sand bass, *P. nebulifer*; sargo, *Anisotremus davidsoni*; kelp surfperch, *Brachyistius frenatus*; señorita, *Oxyjulis californica*; and sheephead, *Pimelometopon pulchrum*, Feder et al. 1974) form relatively long-term (to a few months) spawning aggregations. It is noteworthy that, of these fishes, all except the barred sandbass are midwater, active, species particularly when compared with crevice-dwelling scorpionfish.

Second, few reef associated species move off reefs to spawn. Barred sand bass are one of the few exceptions. These form large spawning aggregations over low relief or flat substrata within the Southern California Bight (Turner et al. 1969). The vast majority of reef dwelling fish are relatively sedentary. Many are either territorial or occupy home ranges. Virtually all stay within the reef vicinity. For these species, spawning takes place within their usual habitats.

Lastly, the California scorpionfish does not have the morphology of a fish given to long movements. Such adaptations can be seen most graphically among the northeast Pacific rockfishes, genus *Sebastes*. Sedentary, territorial species, such as the gopher rockfish, *S. carnatus*, and treefish, *S. serriceps*, are very spiny, squat, and deep-bodied forms. More active, midwater species, such as the yellowtail rockfish, *S. flavidus*, and boccacio, *S. paucispinis*, are more streamlined, with reduced spines (particularly about the head). This trend culminates in the pelagic shortbelly rockfish, *S. jordani*, which resembles a mackerel or sardine. In contrast, California scorpionfish closely resemble the benthic rockfish. Yet, the species seems to move about considerably, even excluding movements to and from spawning grounds. Tagging data from studies of the California Department of Fish and Game show movements as much as 190 km (Hartmann[12]).

Food Habits

We sampled 24 California scorpionfish (TL = 21.2-32.5 cm) with food in their stomachs. Though we captured many hundreds of scorpionfish throughout the Southern California Bight, individuals taken in water deeper than about 16 m regurgitated prey during capture. The 24 individuals with prey represented 68.5% (24 of 35) of all scorpionfish taken in water <16 m.

We have graphically represented prey importance (Fig. 10), using the Index of Relative Importance (Pinkas et al. 1971). Crabs were the most important food item. These were primarily juvenile *Cancer anthonyi*, but we also found a few *Loxyrhynchus* sp., *Randalia ornata*, and *Pagurus* sp. Fishes were second in importance. Recognizable species were the northern anchovy, *Engraulis mordax*, and the spotted cusk-eel, *Chilara taylori*. Octopi, isopods, shrimp (primarily *Alphaeus* sp.), and small pebbles made up the rest of the diet.

[12]A. R. Hartmann, California Department of Fish and Game, Long Beach, CA 90802, pers. commun. June 1984.

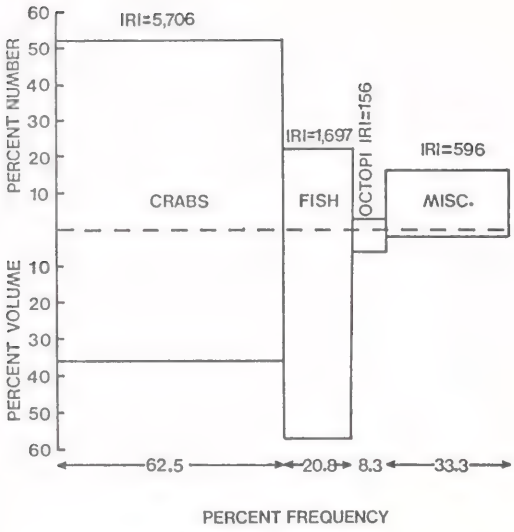

FIGURE 10.—Index of Relative Importance of prey found in stomachs of 24 California scorpionfish, captured in the Southern California Bight.

Turner et al. (1969) examined diets of California scorpionfish living on southern California artificial reefs. They found the species fed almost exclusively upon juvenile *Cancer* crabs during fall and winter; at other times scorpionfish ate octopus and fish. This is similar to our findings, in which juvenile *Cancer anthonyi* were the most important prey. Thus, though the habitat we examined was different from that surveyed by Turner et al., California scorpionfish may sometimes seek out juvenile *Cancer* crabs, regardless of whatever other potential prey are available. When juvenile crabs are not present, California scorpionfish prey on other forms, including octopus and fish.

Limbaugh (1955), Quast (1968c), and Hobson et al. (1981), surveying California scorpionfish over natural rocky reefs, have all reported roughly equivalent food habits, with demersal crustaceans (particularly crabs and shrimps) of most importance, followed by fishes, octopi, and squids. Hobson et al. speculated the species captured most prey at night.

Fishery

Within the Southern California Bight, the California scorpionfish is a relatively minor constituent of the partyboat sportfish catch (Table 7). The species ranked 15th in abundance, comprising about 1.5% of all fishes taken. As scorpionfish were less abundant in the northern part of the Bight, we deleted data from sites north of Pt. Mugu (shown in Figure 1). When species were reranked, scorpionfish moved up to 12th most abundant, forming 1.8% of the catch. Throughout the Bight, over the years 1975-78, the annual contribution of scorpionfish to the total partyboat catch, was fairly constant, hovering at about 1.5% (Fig. 11). Most of the scorpionfish taken aboard partyboats were mature (Fig. 12).

The importance of scorpionfish to the total partyboat fishery varied with season (Fig. 11). During the nearly 4 years of the creel census, scorpionfish contributed most heavily to the catch (as much as 3.0%)

TABLE 7.—The twenty most commonly taken species aboard commercial passenger vessels in the Southern California Bight, April 1975-December 1978. A. Rankings for entire Bight, total number of fish sampled = 342,052. B. Southern California Bight from Pt. Mugu south, total number of fish sampled = 278,664.

Species	No.	%
A		
1. *Sebastes paucispinis*	78,877	23.1
2. *Paralabrax clathratus*	38,315	11.2
3. *Scomber japonicus*	35,072	10.3
4. *Sebastes goodei*	27,218	8.0
5. *Sebastes serranoides*	19,455	5.7
6. *Sarda chiliensis*	16,295	4.8
7. *Paralabrax nebulifer*	13,987	4.1
8. *Sebastes mystinus*	13,646	4.0
9. *Sphyraena argentea*	8,391	2.5
10. *Genyonemus lineatus*	7,841	2.3
11. *Sebastes miniatus*	7,023	2.1
12. *Sebastes chlorostictus*	5,505	1.6
13. *Sebastes hopkinsi*	5,025	1.5
14. *Caulolatilus princeps*	4,990	1.5
15. *Scorpaena guttata*	4,976	1.5
16. *Medialuna californiensis*	3,990	1.2
17. *Sebastes entomelas*	3,969	1.2
18. *Sebastes rubrivinctus*	2,859	0.8
19. *Sebastes elongatus*	2,568	0.8
20. *Sebastes caurinus*	2,513	0.7
B		
1. *Sebastes paucispinis*	61,962	22.2
2. *Scomber japonicus*	33,076	11.9
3. *Paralabrax clathratus*	29,655	10.6
4. *Sebastes goodei*	21,408	7.7
5. *Sarda chiliensis*	16,213	5.8
6. *Sebastes serranoides*	14,987	5.4
7. *Paralabrax nebulifer*	13,371	4.8
8. *Sebastes mystinus*	9,083	3.3
9. *Sphyraena argentea*	8,376	3.0
10. *Genyonemus lineatus*	7,257	2.6
11. *Sebastes miniatus*	5,109	1.8
12. *Scorpaena guttata*	4,880	1.8
13. *Caulotilus princeps*	4,778	1.7
14. *Medialuna californiensis*	3,906	1.4
15. *Sebastes hopkinsi*	3,747	1.3
16. *Sebastes chlorostictus*	3,263	1.2
17. *Sebastes rubrivinctus*	2,381	0.9
18. *Anoplopoma fimbria*	2,279	0.8
19. *Sebastes entomelas*	2,101	0.8
20. *Sebastes constellatus*	2,019	0.7

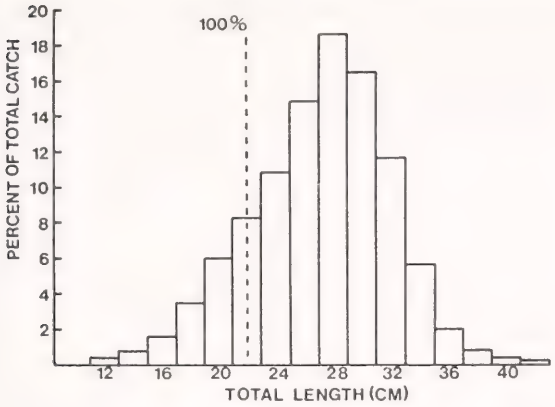

FIGURE 11.—Seasonal distribution of California scorpionfish catch in the southern California partyboat sport fishery, 1975-78.

species is captured by hook and line, gill net, and, rarely, otter trawl. While hook-and-line catches predominate, gill net landings are also important. In a 1984 study, Collins et al.[13] found that scorpionfish were the 10th most abundant species in the California halibut gill net fishery. In recent years, the fishery has been almost entirely limited to the later spring and early summer months (Fig. 13), with catches between June and August accounting for about 80% of the total.

Traditionally, the bulk of California scorpionfish have been caught by a few fishermen specializing in this species. From our observations, it seems likely that the number of specialists has declined markedly since the 1950's. A few vessels of the Newport dory fishery (Cross fn. 8) specialize in fish-

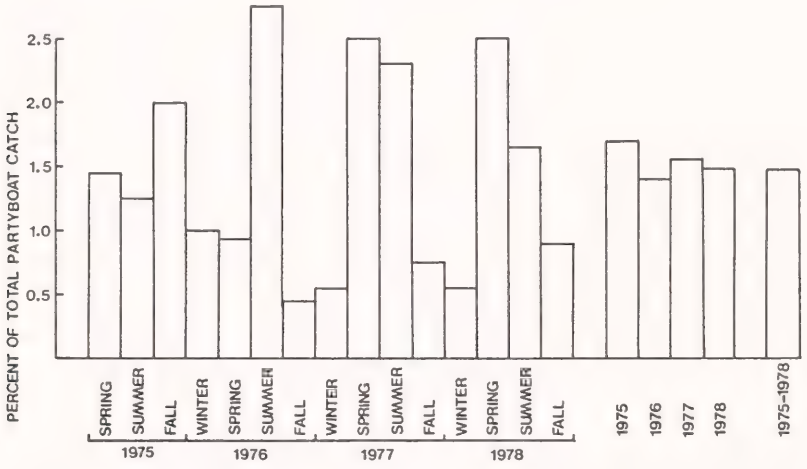

FIGURE 12.—Size distribution (with 100% maturity length) of California scorpionfish taken in the southern California sport fishery, 1975-78.

during spring and summer. This is apparently due to some vessel operators targeting spawning aggregations.

Figure 11 indicates the depths at which California scorpionfish were taken over the years 1975-78. During the May-September spawning season, fish were most abundant in 61-90 and 121-150 m. Relatively few fish were taken between 61 and 150 m from October to April, with catches ranging from 10 to 10^5 times as great in May to September. Similarly, October to April catches were highest in inshore waters.

Historically, California scorpionfish were taken commercially by hook and line and, occasionally, round haul nets (Daugherty 1949). Currently, the

ing for California scorpionfish and their techniques are illustrative. The fishermen concentrate their activities on the spawning grounds offshore of Long Beach—the same area we utilized in our tagging study. As the precise time of fish aggregation varies from year to year, occasional exploratory trips are made to the grounds beginning in May. Most catches begin in June and end in August. Using long lines, the fishermen deploy on the bottom 1,200-2,000 hooks (4/0-5/0 long shank) in 600-1,300 m (1,970-4,265 ft) sets. The hooks (baited with anchovies,

[13]Collins, R. A., M. M. Vojkovich, and R. J. Reed. 1985. Progress Report, Southern California nearshore gill and trammel net study 1984. Calif. Dep. Fish Game, 40 p.

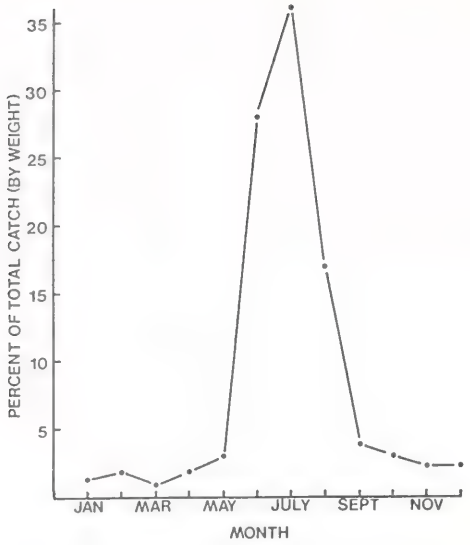

FIGURE 13.—Monthly percentile distribution of the commercial California scorpionfish catch. Based on 1970-84 California commercial landings.

mackerel, or other fish) are usually set about 1 h before sunrise and pulled 1-2 h later. Fishermen report that the fish do not seem to feed well before or after this time.

Traditionally, the Newport fishermen sell their catch to the public on the beach next to the Newport Pier. However, fishermen specializing in scorpionfish often sell their entire catch to fish processors in San Pedro, receiving a relatively high \$1.98-\$2.75/kg (90¢-\$1.25/lb). All commercially caught scorpionfish are sold whole and fresh. Demand is particularly strong within the Asian community.

Over the past 38 yr, commercial landings of California scorpionfish have exhibited considerable fluctuation (Fig. 14), though from relatively high postwar levels, landings have gradually declined, sinking to lowest levels in 1984. Daugherty (1949) noted that fluctuations in California scorpionfish landings seemed more a reflection of fishing effort than of stock size. Certainly, some of the patterns of the last 38 yr reflects fewer fishermen targeting this species. The situation is confounded by a lack of historic population data. However, using the SCCWRP and Orange County Sanitation trawl data (Fig. 4), we note that the rise in scorpionfish population, which peaked in 1982, was matched by a peak in the commercial catch. Conversely, the sharp decline in numbers of trawl-caught fish in 1983-84 was also reflected in the commercial fishery. At least

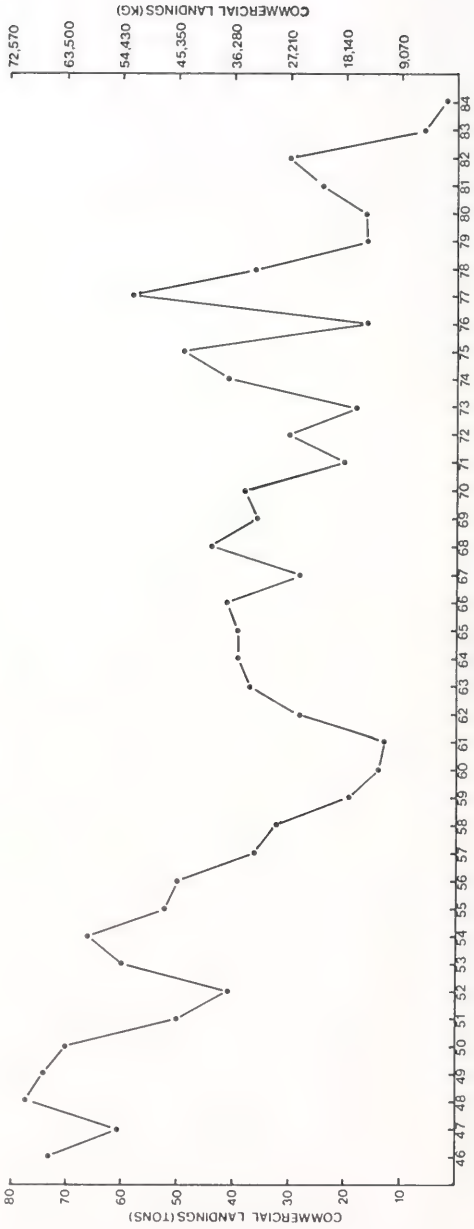

FIGURE 14.—Commercial landings of California scorpionfish caught within California waters, 1953-84.

three sharp catch declines have occurred during or just after warm-water (El Niño) incursions. The major El Niños of the later 1950's and 1983-84 and the lesser one of 1978-79 were all associated with declines in catches. Thus, it seems likely that both variation in fishery effort and fish availability have been responsible for fluctuations in the commercial catch.

As mentioned previously, most of the commercial fishery is concentrated on the spawning grounds, involving rather labor-intensive hook-and-line fishing. Relatively few vessels, primarily small skiffs, specialize in this fishery. While fisheries which occur primarily on spawning grounds are quite susceptible to rapid depletion, the relative inefficiency of this fishery and the low effort level may preclude this event. However, the introduction of other fishing techniques, such as gillnetting or trawling, might cause problems. At present, most trawling is conducted in the upper part of the Southern California Bight, where spawning aggregations are either small or absent. Trawling over spawning grounds would likely lead to a rapid decline in scorpionfish numbers.

Similarly, sportfishing can locally decrease the numbers and mean lengths of popular sport species. This is particularly true of the partyboat sport fishery, where vessels carrying 40 or more passengers may fish the same reef day after day. Particularly susceptible are the inshore rockfishes (Scorpaenidae: *Sebastes*) many of which maintain home ranges or territories on shallow reefs (Love 1978, 1980; Larson 1980). On some heavily fished reefs in southern California, only juveniles of some rockfish species remain—larger individuals are caught as soon as they are large enough to take a hook. However, because California scorpionfish are quite mobile—not permanently tied to a particular reef—they are not as susceptible to depletion as other inshore members of their family.

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BIAS AND VARIANCE IN ALLEN'S RECRUITMENT RATE METHOD

J. W. Horwood[1]

ABSTRACT

The method of estimation of the recruitment rate of a population based upon the methodology of Allen is reviewed, and a simpler formulation is presented. The estimator is evaluated for bias and variability. If the recruitment pattern at age is constant with time, the technique shows no bias provided the age of first full recruitment is not underestimated. Use of age-length keys will tend to spread partially recruited ages upwards so the age of first full recruitment should accommodate this. An approximate analytical formula for the variance of the estimated recruitment rate is given, and this shows that variance decreases with increasing second year catches.

If recruitment to a fishery changes such that it occurs at an earlier age with time, then high values of recruitment rate are given and vice versa. This could be interpreted erroneously as an increasing or decreasing population growth rate, if it was assumed that the pattern of new recruitments at age had been constant. It is also found that a fluctuating recruitment pattern will give a negatively biased rate. These last considerations suggest that the method should not be used unless a constant recruitment pattern can be established. For a series of years of data other techniques should be used.

Allen (1966, 1968) introduced a technique for the estimation of the proportion of new recruits to total recruits in an exploited stock. This statistic is particularly useful since it is necessary for the simulation of stock dynamics and hence it is used in the estimation of stock size. As proposed by Allen the statistic is obtained directly from the catch of the previous 2 years, and this is in contrast to estimates obtained by virtual population analysis, which requires several years of data for a comparable estimate to converge to a satisfactory answer. Allen termed this parameter r_{II} but here it will be denoted by r. The only data needed to calculate this recruitment rate are the proportions of catch at age for 2 consecutive years, and a knowledge of the age of first full recruitment. Allen (1973) used this method to calculate the recruitment rates of fin whales in the Antarctic and so constructed a stock and recruit relationship and estimated stock sizes. The use of Allen's method of obtaining recruitment rates has been advocated by Ricker (1975) and Gulland (1977: Chapter 1 by Ricker, Chapter 4 by Gulland, Chapter 14 by Allen and Chapman). The method has been used extensively in stock assessments by the International Whaling Commission but often has given average values that were thought to be unreasonably low. This can be seen for sei whales in Ohsumi (1978) and for minke whales in Chapman (1983). In addition, the rates have been very variable even with moderately high catches (Ohsumi 1978; Allen 1982). Some properties of the estimate have been considered. Ricker (1975) investigated the effect of changes in some of the population parameters and found a negative bias if the first age of full recruitment was underestimated, and Allen (1981) looked at the sensitivity of the method to variable catches at age and concluded that although variability of the estimate was high for catches less than a few hundred, the bias was small even for low catches. This still left unresolved the question of why the estimated recruitment rates were often so low and why they were more variable than Allen's (1981) simulations predicted. Ohsumi's results gave coefficients of variation over 200%, whereas Allen's simulations gave about 75% if catches were low.

This study investigates the behavior of the estimated recruitment rate from Allen's model. The estimator is fully introduced in order to demonstrate that the existence of a free and selectable parameter (Allen's T) is erroneous; once established the estimator then reduces to a simple form. A typical age-structured model is introduced and the effects on the estimated recruitment rate of changes from year to year of demographic parameters of the model are investigated. The effect of sampling variability in the number of animals caught at age is reviewed in relation to bias and variance of the estimate, and an expression for the approximate analytical variance of the recruitment rate is pre-

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sented. However the most important finding is that it is shown that trends in recruitment rate and changes in selection pattern are confounded.

DERIVATION OF RECRUITMENT RATE ESTIMATOR

Allen's (1966, 1968) definition of recruitment rate is the proportion of new recruits to total recruited stock, that is, the number of animals newly available for capture compared with the total available in that year. It is explicitly defined through Equation (1) below. Retaining the same nomenclature as Allen (1966) let us define the following terms:

$N_{i,t}$: numbers in the population of age i in year t,
$C_{i,t}$: catch in numbers of age i in year t,
$U_{i,t}$: proportion of age group i in year t that are exploitable, i.e., recruited,
$P_{i,t}$: proportion of the total catch from age i in year t,
$Q_{i,t}$: proportion in the catch of year t from all fully recruited age groups $\geq i$,
CT_t : total catch in year t,
M : instantaneous natural mortality rate,
F_t^a : instantaneous fishing mortality rate on fully recruited ages in year t, ages $i \geq k$,
Z_t^a : instantaneous total mortality rate, $F_t^a + M$, on fully recruited ages,
F_t^j, Z_t^j : instantaneous fishing and total mortality rates on pre-fully recruited ages, ages $i < k$,
F_t, Z_t : instantaneous mortality rates if there are no differences between juvenile and adult rates,
k : age of first full recruitment, $U_{i,t} = 1.0\ i \geq k$,
r_t : net recruitment rate in year t.

Let us define $\phi_t^j = F_t^j(1.0 - \exp(-Z_t^j))/Z_t^j$ and similarly for ϕ_t^a. By definition, the recruitment rate is

$$r_2 = \frac{\text{new recruits}}{\text{total exploitable}} = \frac{\sum_{i=x}^{k} N_{i,2}\, U_{i,2} - (\exp(-Z_1^j)) \sum_{i=x}^{k-1} N_{i,1}\, U_{i,1}}{\sum_{i=x}^{\infty} N_{i,2}\, U_2}, \qquad (1)$$

where x is the age of first partial recruitment. This can be rewritten as

$$r_2 = \frac{\sum_{i=x}^{k-1} C_{i,2}/\phi_2^j + C_{k,2}/\phi_2^a - (\exp(-Z_1^j)) \sum_{i=x}^{k-1} C_{i,1}/\phi_1^j}{\sum_{i=x}^{k-1} C_{i,2}/\phi_2^j + \sum_{i=k}^{\infty} C_{i,2}/\phi_2^a}.$$

Multiplying top and bottom by ϕ_2^j/CT_2 gives

$$r_2 = \frac{\sum_{i=x}^{k-1} P_{i,2} + P_k\, \phi_2^j/\phi_2^a - (\exp(-Z_1^j)) \sum_{i=x}^{k-1} C_{i,1}\, \phi_2^j/\phi_1^j\, CT_2}{\sum_{i=x}^{k-1} P_{i,2} + (\phi_2^j/\phi_2^a) \sum_{i=k}^{\infty} P_{i,2}}.$$

Note that $\frac{Q_{k+1,2}}{Q_{k,1}} = \frac{(\sum_{i=k+1}^{\infty} C_{i,2})\, CT_1}{(\sum_{i=k}^{\infty} C_{i,1})\, CT_2} = \frac{CT_1\, \phi_2^a \exp(-Z_1^a)}{CT_2\, \phi_1^a}.$

Therefore

$$r_2 = \frac{\sum_{i=x}^{k-1} P_{i,2} + P_{k,2}\,\phi_2^j/\phi_2^a - Q_{k+1,2}\left(\sum_{i=x}^{k-1} P_{i,1}\right)\phi_2^j\phi_1^a \exp(Z_1^a - Z_1^j)/(Q_{k,1}\,\phi_1^j\phi_2^a)}{\sum_{i=x}^{k-1} P_{i,2} + (\phi_2^j/\phi_2^a)\sum_{i=k}^{\infty} P_{i,2}}. \quad (2)$$

Compare this result with that given by Allen (1966, 1968). He gives

$$r_2 = P_{1,2} - \sum_{i=1}^{k-1} (1.0 - T_1/B_{i,1})\cdot P_{i+1,2},$$

where $B_{i,1} = P_{i+1,2}\cdot Q_{k,1}/(P_{i,1}\cdot Q_{k+1,2})$

$$T_t = \exp(Z_t^a - Z_t^j).$$

Consequently,

$$r_2 = \sum_{i=x}^{k} P_{i,2} - T_1(Q_{k+1,2}/Q_{k,1})\sum_{i=x}^{k-1} P_{i,1}. \quad (3)$$

To satisfy the above Equations (2) and (3) it is found that $\phi_2^j/\phi_2^a \equiv 1.0$. That is, the proportion fished in the two recruited age groups in the second year must be the same. If it is then assumed that the natural mortality rate, M, is the same in each group, then it is necessary that $F_2^j \equiv F_2^a$. From Equation (2) we then have

$$r_2 = \sum_{i=x}^{k} P_{i,2} - T_1\left(\sum_{i=x}^{k-1} P_{i,1}\right)(Q_{k+1,2}/Q_{k,1})\phi_1^a/\phi_1^j.$$

Consequently to satisfy Allen's model, Equation (3), it is also necessary that $\phi_1^a/\phi_1^j \equiv 1.0$, and as above this implies $F_1^j \equiv F_1^a$. Hence $Z_1^a = Z_1^j$ and $T_1 = \exp(Z_1^a - Z_1^j)$ is necessarily unity, and there is no flexibility in the choice of T as Allen (1966, 1968) and Ricker (1985) suggest.

If one then assumes that, within each year, the mortality rate of all recruits is similar, then Equation (2) reduces to a very simple form

$$r_{t+1} = \alpha - \beta(1 - \alpha)/(1 - \beta),$$

where $\alpha = \sum_{i=1}^{k} P_{i,t+1}$

$$\beta = \sum_{i=1}^{k-1} P_{i,t}. \quad (4)$$

DEVELOPMENT OF A VALIDATION PROCEDURE

In order to test the robustness of the estimator given by Equation (4) we need a population model. If in year 1 the population is assumed to have a stable age structure and has been increasing at a rate of λ per year, such that the population vector,

$$N_{t+1} = \lambda N_t,$$

and where the mortality rate, Z, has been constant over time, then with an arbitrary number of 1-yr olds the numbers at age in year 1 can be calculated from the recurrence relationship:

$$N_{1,1} = 5{,}000.$$

$$N_{i+1,1} = N_{i,1}[U_{i,1}\exp(-Z_1) + (1.0 - U_{i,1})\exp(-M)]/\lambda,$$

$$N_{21,1} = N_{20,1}\cdot\exp(-Z_1)/\{\lambda(1.0 - \exp(-Z_1))\}.$$

It is assumed that $U_{20,1} = 1.0$, i.e., $k \leqslant 20$ and N_{21} is a "plus-group" of ages $\geqslant 21$. The age subscripts have now been dropped from Z and F. Consequently the numbers in the second year are given by

$$N_{1,2} = \lambda\cdot 5{,}000.$$

$$N_{i+1,2} = N_{i,1}[U_{i,1}\exp(-Z_1) + (1.0 - U_{i,1})\exp(-M)]$$

$$N_{21,2} = (N_{20,1} + N_{21,1})\exp(-Z_1)$$

$$P_{i,t} = (N_{i,t}\,U_{i,t})/\sum_{i=1}^{21}(N_{i,t}\,U_{i,t}). \quad (5)$$

If we wish to consider the effects of stochastic catches at age or problems in aging, then $P_{i,t}$ becomes a variable, $\bar{P}_{i,t}$, and can be expressed in terms of the catch, so that

$$\bar{P}_{i,t} = C_{i,t}/CT_t,$$

where $C_{i,t}$ is determined as an independent random variable. For the expected catch at age, $m \geq 50$ $C_{i,t}$ is distributed as $N[m_{i,t}, m_{i,t}(1 - P_{i,t})]$ where $P_{i,t}$ is calculated from Equation (5), and for $m < 50$ as Poisson $[m_{i,t}]$. m is obtained as

$$m_{i,t} = F_t(1.0 - \exp(-Z_t))\, N_{i,t}\, U_{i,t}/Z_t,$$

and

$$CT_t = \sum C_{i,t}.$$

If aging of the catch introduces bias or variance this can be investigated using a matrix A where the element $a_{i,j}$ is the probability that an animal of true age i will be called j. The new catch at allocated age can be given by C' where

$$C'_t = A\, C_t,$$

and where C is the column vector of catch at age.

From the validation model the true recruitment rate can be calculated as

$$\frac{N_{1,2}U_{1,2} + \sum_{i=1}^{k-1} (N_{i+1,2}U_{i+1,2} - N_{i,1}U_{i,1} \exp(-Z_1))}{\sum_{i=1}^{21} N_{i,2}U_{i,2}} \qquad (6)$$

It can be easily shown that, for $U_{i,1} = U_{i,2}$ $N(t = 1)$ in a stationary age composition, this reduces to

$$(\lambda - \exp(-Z_1))/\lambda. \qquad (7)$$

In the following tests the results using Equations (6) and (4) will be compared when parameters are changed from year to year or when variability is introduced. In all tests $F_1 = 0.05$ and $M = 0.05$.

RESULTS

The results of comparing the true recruitment rate from Equation (6) with those obtained from Equation (4) are given below, for the cases when the fishing mortality is different in 2 adjacent years, for $\lambda \neq 1$, and for the age at first full recruitment (k) incorrectly chosen when $U_{i,2} = U_{i,1}$ (sections i - iii below). Section iv considers the effect of variability and biases in the age determination of the catch and section v considers stochastic effects, all with $U_{i,2} = U_{i,1}$. Section vi considers the effects of $U_{i,2} \neq U_{i,1}$.

(i) $F_2 \neq F_1$

From Equation (6) it is evident that the value of F_2 ($F_2 \neq 0$) does not affect the recruitment rate and this is reflected in Equation (4) where only proportions in the catch each year are needed. The value does however affect the variance of r as shown later. This was also noted by Ricker (1975).

(ii) $\lambda \neq 1.0$

Equation (7) shows that r is a funtion of λ, the rate of increase of the population given F_1. Equation (4) accurately gives the true value of r irrespective of λ or F_2.

(iii) k - Incorrectly Chosen

Let k' be the selected age at first full recruitment. If $k' \geq k$ then Equation (4) gives the same rate as Equation (6). As a confirmation of Ricker's (1975) findings it is easy to show that in the extreme case of knife-edge recruitment k' can be $\geq k$ and that if k' is $< k$ then no new recruitment is detected. For $U_i = 0.1i$, $i = 1$ to 10 and $U_i = 1.0$, otherwise Table 1 shows the reduction in r using Equation (4) as k' is reduced from its true value at $k = 10$. The reduction is substantial and the effect on the estimated net recruitment rate, r', is more so. r' is calculated as (Chapman 1983)

$$r' = r - 1 + \exp(-M).$$

It can be seen that in this example, which is not unlike many examples in whale assessments, an error of 1 year would reduce r' by 20%. (It is worth noting that this equation for the net recruitment rate is approximate and underestimates the true net rate by about the product of F and M or F and Z depending

TABLE 1.—Reduction in recruitment rates (r) as k' is incorrectly chosen $< k = 10$, and net recruitment rate, r'.

k'	10	9	8	7	5	3
r	0.095	0.086	0.077	0.068	0.051	0.032
r'	0.046	0.037	0.028	0.022	0.002	−0.016

on when the catches are removed from the population.)

(iv) Aging of Catch Biased

If aging is biased such that each age is wrongly allocated to another specific age then the matrix A may look like Table 2(a), which would indicate that all animals age i were called $i + 1$ for $i = 1$ to 4. If the true age of first full recruitment, k, is 3 and this was used in Equation (4) an underestimate would result as described above. This may occur if k is obtained independently of the catch data. If however the catch data are used to estimate k this will also be aged incorrectly with the result that the estimate of r is correct. In the example $k' = 4$ and this value used in Equation (4) yields the correct answer.

TABLE 2.—Matrix A of allocated age against true age.

(a)	(0	0	0	0	0)	(b)	(1	0.2	0	0	0)
	(1	0	0	0	0)		(0	0.6	0.2	0	0)
	(0	1	0	0	0)		(0	0.2	0.6	0.2	0)
	(0	0	1	0	0)		(0	0	0.2	0.6	0.2)
	(0	0	0	1	1)		(0	0	0	0.2	0.8)

Often an age-length key is used to age the catch. This implies that an animal of true age i will be allocated to age j with a probability distribution centered upon i. Table 2(b) shows matrix A in such a case. If, in this example, $k = 3$, the spreading of some of the catch at age 3 into age 4 means a bias will result from the omission of this group. Consequently the k used in Equation (4) needs to be 4 to avoid a negative bias. The value of k used needs to be such as to ensure that all partly recruited ages are counted and if age-length keys are used, it may have to be substantially higher than the true age of first full recruitment.

(v) Stochastic Results

In this section we consider the biases introduced by variability occurring in the system.

Variance in Catch at Age

Variance in catch at age in the first year was modelled with either a Poisson or Normal distribution as previously described. For the second year the age distribuion was found given these stochastic catches and an expected catch in year 2 was obtained given F_2. From the expected $C_{i,2}$ a second stochastic set of catches was obtained. This was repeated for 50 pairs of years with $U_i = 0.2(5 - i)$ for i from 6 to 10 and 1.0 for older ages.

For a range of λ and F_2 the average value of r, calculated from Equation (4), was accurate to within a few percent either way of the true value of r. This is in agreement with the findings of Allen (1981). However, even for small values of F_1 and F_2, and hence low catches, there was no evidence of a general bias; this is contrary to the findings of Allen (1981).

Variance of r

From the population model the variance of r can be calculated for given F_1 and F_2. For each of the 50 simulations described above the mean and variance of r was calculated. The coefficients of variation agreed well with those described by Allen (1981, table 1) ranging from 0.15 for a second year catch of 2,500 to 0.76 for a catch of 75.

A theoretical variance is derived below.

Let us define $\theta_t = Z_t/\{F_t(1.0 - \exp(-Z_t))\}$

and $\theta = \theta_1/\theta_2$.

Let x = the age of first partial recruitment, remember $U_{i,1} = U_{i,2}$, and CT_t is the total catch in year t. Then from Equation (6) it can be seen that r can be written as

$$r_2 = (\sum_{i=1}^{k} C_{i,2} - \theta \exp(-Z_1) \sum_{i=1}^{k-1} C_{i,1})/CT_2.$$

Note that $E(C_{i,2}) = N_{i,2}U_i/\theta_2 \qquad i = x + 1 \text{ to } 20$

$$= \xi_i \, C_{i-1,1}$$

where $\xi_i = \theta(U_{i-1} \exp(-Z_1) + (1.0 - U_{i-1}) \exp(-M)) \, U_i/U_{i-1}$, and writing the catch from the fully recruited plus group at time 2 in terms of that at time 1 we get

$$E(C_{21,2}) = \xi_{21} \, C_{20,1} + \xi_{22} \, C_{21,1},$$

where $\xi_{22} = \theta \exp(-Z_1)$.

No prior information is known about $N_{i,1}$ and so we must assume that $E(C_{i,1}) = C_{i,1}$. If $C_{i,1}$ is assumed to be a Poisson variable with parameter $(C_{i,1})$ the sample catch then $C_{i,2}$ can be assumed to be a compound-Poisson variable with a relationship that can be approximated by

$$C_{i,2} = \zeta_i C_{i-1,1} + \varepsilon_i, \qquad i = x + 1 \text{ to } 20,$$

and

$$C_{21,2} = \zeta_{21} C_{20,1} + \zeta_{22} C_{21,1} + \varepsilon_{21} + \varepsilon_{22},$$

where $E(\varepsilon_i) = 0$ and $\text{var}(\varepsilon_i) = (\zeta_i + \zeta_i^2) C_{i-1,1}$.

Consequently,

$$r_2 = [C_{x,2} + \sum_{i=x}^{k-1} (\zeta_{i+1} - \theta \exp(-Z_1)) C_{i,1} + \sum_{i=x+1}^{k} \varepsilon_i]/$$

$$[C_{x,2} + \sum_{i=x}^{21} \zeta_{i+1} C_{i,1} + \sum_{i=x+1}^{22} \varepsilon_i].$$

For any given vector N_1 and fixed Z_1 and Z_2 the above terms are independent and the approximate variance can be given by

$$\begin{aligned}\text{var}(r_2) = {} & \text{var}(C_{x,2})(\partial r/\partial C_{x,2})^2 \\ & + \sum_{i=x}^{21} \text{var}(C_{i,1})(\partial r/\partial C_{i,1})^2 \\ & + \sum_{i=x+1}^{21} \text{var}(\varepsilon_i)(\partial r/\partial \varepsilon_i)^2 \\ = {} & [C_{x,2}(1 - r)^2 \\ & + \sum_{i=x}^{k-1} \{\zeta_{i+1}(1 - r) - \theta \exp(-Z_1)\}^2 C_{i,1} \\ & + \sum_{i=x}^{k-1} (1 - r)^2 (\zeta_{i+1} + \zeta_{i+1}^2) C_{i,1} \\ & + \sum_{i=k}^{21} r^2 (\zeta_{i+1} + 2\zeta_{i+1}^2) C_{i,1}]/(CT_2)^2. \quad (8)\end{aligned}$$

Comparison of the simulated variances, with the above pattern of recruitment and $k = 10$, with those predicted from Equation (8) showed the analytical variance to be a very good approximation, averaging about 0.96 times the simulated variances. However, with $k = 12$ the analytical variance was only 0.70 times the simulated variance. It is clear from Equation (8) that the variance will decrease as the square of the second year catch increases but the first year catches play a more linear role, except through the interactions of ζ and θ with the first year catch.

Equation (8) also shows there is a cost involved with increasing k. This is desirable to avoid any bias, but if too few age classes are considered to be fully recruited, then variance increases. In the example considered, raising k from 10 to 12 yr increased variance by 40% and the simulated variances show the increase may even be greater.

Additional simulations also revealed that the use of an age-length key might reduce variance by smoothing out real differences in catch at age, but the reduction was nullified by the additional variance due to increasing k.

(vi) $U_{i,2} \neq U_{i,1}$

Equation (6) still allows a true recruitment rate to be calculated in this case and Allen's (1966) derivation allows $U_{i,2} \neq U_{i,1}$. As k should not be underestimated when used in Equation (4), then k can be defined as the larger of the two ages of first full recruitment in years 1 and 2.

In this trial an initial stable age distribution was prescribed with $\lambda = 1.0$, $F_1 = 0.05$ and

$$\begin{aligned} U_{i,1} &= 0 && i < 5 \\ &= (i - 5) \times 0.2 && i = 5 \text{ to } 10 \\ &= 1.0 && i > 10. \end{aligned}$$

A deterministic catch $C_{i,1}$ was obtained given F_1 and the population vector N_2 found. The catch and population vector in year 2 was then calculated with $F_2 = F_1$ and a changed $U_{i,2}$,

$$\begin{aligned} U_{i,2} &= 0 && i < k_2 - 5 \\ U_{i,2} &= (i + 5 - k_2) \times 0.2 && i = k_2 - 5 \text{ to } k_2 \\ U_{i,2} &= 1.0 && i > k_2. \end{aligned}$$

With $U_{i,3} = U_{i,1}$ and $F_3 = F_1$ a third catch was obtained.

From this simulation two recruitment values can be obtained, r_2 and r_3, using Equation (4). The results are given in Table 3 and demonstrate 1) the effect of recruitment occurring earlier in the second year (r_2 with $k_2 < 10$, and r_3 with $k_2 > 10$); 2) the effect of recruitment occurring later in the second year (the converse); and 3) the effect of the age of recruitment fluctuating about an average k to $\pm|k - k_2|$.

Under these conditions Equation (4) accurately gives the proportion of new recruits in the population and, as expected, if selection and recruitment

occur at an earlier age in the second year then a large burst of new recruits will appear. If selection occurs much later, then even the recruits of the previous year will not be seen, giving the negative values. Such a feature was noted by Holt and de la Mare (1983). Horwood et al. (1985) fitted a selection pattern with age that was constant over time for minke whales of the Southern Hemisphere and presented the residual differences. A substantial switching of effort on to different age classes was found over a period of years, and it was shown that this was reflected in the calculated recruitment rates. These residuals and recruitment rates are shown in Table 4 and clearly illustrate the character of the estimate.

The problem is then not of calculation but of interpretation, in that we do not know selection has changed, and in using this technique it is assumed that the recruitment pattern is constant. A decreasing trend in recruitment rate will be interpreted as a decline in the true rate and not as an increasing age at recruitment and vice versa. As Table 3 shows these rates differ greatly from the 0.095 for constant selection, being much higher or lower depending on the trend in recruitment pattern. Consequently a systematic change in recruitment to the fishery will cause substantial problems in interpretation of the recruitment rates.

Table 3 also indicates what is likely to occur if the age of recruitment systematically fluctuates about a set pattern. It might be hoped that the r values would average to a useful measure of mean recruitment rate. For $k_2 = 6$ the recruitment occurs much earlier in year 2, giving a high r_2, and returns to normal in year 3, giving a low r_3. However, the average (0.033) is much smaller than the 0.095 and the approximate net recruitment rate is negative. A similar feature is seen for $k_2 = 14$, but as $|k_2 - 10|$ tends to zero the discrepancy is less. If the system fluctuated so that we had a series $k(t) = 10, 6, 10, 14$, and 10, an approximate average value of r would be the average of the four values of r on Table 3 ($0.367, -0.301, -0.340, 0.397 = 0.031$), and the approximate symmetry gives a similar feature of low average recruitment rates.

One way of using the recruitment rates would be to multiply the net recruitment rate by an estimated population size obtained over the same period to give a catch quota which should approximately stabilize the population. From the simulation the average of the recruited population in years 1, 3, and 4 has been found. This is very near to the average of the 4 years if the basic recruitment pattern is assumed for the second year. A catch was then found which would make the recruited population in year 5 the same

TABLE 3.—Recruitment rates calculated from Equation (4) for the model described in section vi. k is the age of first full recruitment used in Equation (4), k_2 is the first full recruitment in year 2. $\bar{r}$ is the average of the two values and nr is the average approximate net recruitment rate.

k_2	k	r_2	r_3	$\bar{r}$	nr
6	10	0.367	−0.301	0.033	−0.015
7	10	0.311	−0.194	0.058	0.009
8	10	0.247	−0.093	0.077	0.028
9	10	0.176	0.004	0.090	0.041
10	10	0.095	0.095	0.095	0.046
11	11	0.004	0.181	0.092	0.043
12	12	−0.099	0.260	0.080	0.031
13	13	−0.213	0.332	0.059	0.010
14	14	−0.340	0.397	0.028	−0.020

TABLE 4.—Direction of residuals after fitting a time constant selection at age to minke whale data showing switching of fishing selection across ages with time. Recruitment rate (r) values reflect this switching. (After Horwood et al. 1985.)

Age	1974/75	1975/76	1976/77	1977/78	1978/79	1979/80	1980/81	1981/82
1	+	+	+	−	+	−	−	−
2	+	+	+	−	+	−	−	+
3	−	+	+	−	+	+	−	+
4	−	+	+	−	+	+	−	+
5	−	−	+	+	−	−	−	+
6	−	−	+	+	−	−	−	+
7	−	−	+	+	−	−	−	−
8	−	−	+	+	−	−	−	−
9	−	−	−	+	−	+	+	−
10	−	−	−	+	−	+	+	−
11	−	−	−	+	−	+	+	−
12	+	−	−	+	−	+	+	−
13	−	−	−	+	−	+	+	−
14	+	−	−	+	−	+	+	−
15	+	+	−	+	−	+	+	−
16	−	+	−	+	−	+	+	−
r values	0·12	0·18	0·01	0·19	−0·08	−0·00	0·27	

size as this average. The ratio of this catch to the average population is the net recruitment rate that we would wish to use; these values varied from 0.04 (k_2 = 6) to 0.05 (k_2 = 14). This confirmed that the distortion of the age structure and population size by the change in selection had very little effect and that a value of r of 0.095, a net rate of 0.046, would be needed to calculate a stabilizing catch. The Table 3 averages are much smaller and we must conclude that if there is no trend in recruitment but a fluctuation of more than 1 year then the average estimated rates will be largely but undeterminably negatively biased, even if k is not underestimated. A 50-yr simulation confirmed this to be true.

As can be gleaned from the above, selection plays an important role in determining r. However, this technique treats overlapping pairs of years as being independent and implies a selection pattern for a pair of years, say 1980 and 1981 and a different one for years 1981 and 1982; these assumptions may be inconsistent. The difference may be small or large but there is no criterion for acceptability. Some current techniques take arrays of catch-at-age data and obtain best fits to the overall pattern (Beddington and Cooke 1981; Pope and Shepherd 1982), and Pope and Shepherd reduced consideration to two parameters. What is clear is that selection and recruitment or fishing rates are confounded, and these latter techniques make the assumptions clearly and would be expected to replace analyses of pairs of years.

CONCLUSIONS

If the recruitment pattern to the exploited population is constant then the following conclusions may be stated.

1. The "T" of Allen's technique is shown to be necessarily unity and this gives rise to Equation (4) for the estimation of recruitment rate.
2. If the age of first full recruitment is selected correctly then calculated recruitment rates are unbiased for changing fishing efforts or for an increasing or decreasing population.
3. If the age of first full recruitment is overestimated then an unbiased recruitment rate is found. If it is underestimated then a negative bias ensues. Inspection of Equation (4) however would caution use of an assumed high value of k, such that α and β were near unity, and this is reflected in the higher variances given by the approximate variance formula.
4. Aging bias and the use of age-length keys may spread the partially recruited age groups into allocated higher ages. The age of first full recruitment should be high enough to encompass this spreading.
5. No bias was detected in recruitment rates from a series of stochastic simulations although Allen (1981) found a small negative bias with low catches. As found by Allen (1981) coefficients of variation of the recruitment rates are high.
6. Equation (8) provides an approximate formula for the variance of the recruitment values given a fixed effort in the pairs of years. To use this the recruitment pattern needs to be estimated from the data as described by Allen (1966).

If the recruitment pattern is not constant, serious biases follow:

7. If there is a trend to earlier recruitment over a period of years high recruitment values will be seen and vice versa. These are likely to be interpreted as true increases or decreases.
8. If the recruitment pattern fluctuates about a mean then the net or gross average recruitment rate will be negatively biased, the bias increasing with the amplitude of the fluctuations. It is likely that many of the very low rates found by the International Whaling Commission are due to this feature.
9. These last two points indicate that for the technique to be useful it is necessary to establish that the recruitment pattern has been constant. This is likely to prove difficult and consequently much of the value of this simple method is lost.
10. For groups of years of data, alternative techniques should be investigated.
11. Finally it appears that the Allen recruitment rate, as calculated in this study or through Allen's original equations with T = 1, should be used with great care. It is subject to large and undeterminable biases and large variances. Where possible other techniques should be used.

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FECUNDITY AND SPAWNING FREQUENCY OF THE HAWAIIAN ANCHOVY OR NEHU, *ENCRASICHOLINA PURPUREA*

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ABSTRACT

Female nehu can begin spawning at 35 mm standard length; almost all fish over 40 mm SL from Kaneohe Bay were mature and in spawning condition. Mature females were found in all months of the year. Females from summer (May-October) had higher fecundity and relative cost per batch than fish from winter (November-April). In nehu and most other anchovies, fecundity appears to increase exponentially with weight. Nehu appear to be distinguished from other species by a higher exponent and consequently greater increase in relative fecundity over the reproductive size range. Nehu spawn during a short period 1 or 2 hours after sunset and begin hydrating ova only a few hours before spawning. Data on presence or absence of hydrated ova or postovulatory follicles along with differences in oocyte size in fish collected from throughout the diel cycle indicated that, after spawning, nehu can ripen a new batch of oocytes in 2 days and that most females spawn every other day. The estimated requirements for continued spawning at this rate indicate that individual variation in recent feeding success or stress could be responsible for observed scatter about fecundity-weight relationships and deviation from the normal spawning frequency.

The nehu, *Encrasicholina purpurea*, is a small anchovy endemic to the Hawaiian Islands. It is one of the dominant planktivorous fishes in enclosed, semi-estuarine areas and is the major source of bait for the local skipjack tuna fishery. Nehu are short-lived; growth increments on otoliths indicate a maximum age of about 6 mo (Struhsaker and Uchiyama 1976). Leary et al. (1975) showed that nehu can reach maturity at 35 mm standard length (SL) and presented fecundity data for 41 females. Leary et al. found very few females with hydrated ova and, on that basis, suggested that nehu spawn only once per lifetime.

Reexamination of Leary et al.'s (1975) conclusions was prompted both by the great variability in their fecundity vs. weight relationship and by discovery in recent collections that female nehu with hydrated ova are not at all rare, but rather are found only at restricted times of the day. This paper presents results of more detailed investigations of fecundity and spawning frequency in nehu in order to compare and contrast aspects of reproductive output of a tropical anchovy with those of better studied temperate species.

MATERIALS AND METHODS

All nehu examined for this study were collected from Kaneohe Bay, HI. Day samples were collected by beach seine or dip net in shallow water (1-2 m deep) or were taken from bait recently collected from similar areas by skipjack tuna vessels. Night samples were taken by blind sets with a ca. 67 m long by 13 m deep purse seine over deeper (12-14 m) areas of the bay. Forty-four night samples and two day samples were taken in 1974-79, while 5 night samples and 18 day samples were taken in 1983-85. Samples with adult nehu were available from all months of the annual cycle and, for most months, from at least two different years. One or more samples with adults were available from all hours of the diel cycle except the period between midnight and dawn, when there were few samples and very few adults collected.

In order to follow short-term oocyte development in the same group of fish, on two occasions a school of nehu was surrounded with a 60 m long beach seine in shallow water and sampled initially and twice later in the day. Samples were taken at the hours of 1300, 1500, and 1700 on 13 January 1984 and at 1000, 1300, and 1600 on 27 January 1984. Although the school was obviously disrupted by initial surrounding and subsequent dipnetting of samples, the fish held in the net appeared to resume normal daytime behavior shortly after each disturbance and spent most of the time loosely schooled with other nehu on the outside of the net. The oocyte size-frequency data from these samples did not differ in any obvious manner from data taken from other

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samples at approximately the same times on other days; consequently, the data from these "enclose and hold" samples were pooled with the others for all analyses.

Time of collection was recorded as the beginning of the set of the net; usually 15-30 min elapsed before the sample was actually preserved. For samples taken from skipjack tuna vessels, the time of collection was often only known within ±15 min and the delay between collection and preservation of the sample was often somewhat longer than 30 min.

For analyses of oocyte development rate and spawning frequency, collection time was adjusted to hours since the most recent spawning. Data on appearance of newly spawned eggs in the plankton (Clarke unpubl. data) indicate that spawning begins 1-2 h after sunset and is nearly over in about an hour; the delay after sunset is greatest during the summer. For samples considered here, spawning time was assumed to be 1 h after sunset for dates between mid-October and the end of April and 2 h after sunset for the remainder of the year. Given the frequent uncertainty in actual time of capture, this crude correction for spawning time was satisfactory for the purposes of the present study.

All specimens were preserved and held in ca. 4% formaldehyde/seawater solution. The recently collected samples were held at least 1 wk before measurement and further analyses; by this time most shrinkage in length had occurred. Although the older samples had been in preservative for several years, there was no evidence that long-term storage had affected any parameters considered here, e.g., length-weight relationships were similar for both recent and older samples.

For each sample, standard length (SL) of all or a subsample of ca. 100 specimens was measured to the nearest mm. Individuals for further examination were selected from throughout the size range of nehu >35 mm SL in the sample. The selected individuals were measured to the nearest 0.5 mm, opened, and the gonads examined under a dissecting microscope. Females were classed as immature —ovaries translucent and maximum oocyte length <0.40 mm; mature—ovaries mostly opaque, oocytes visibly yolked and over 0.40 mm; or hydrated—mature and at least some oocytes with translucent, globular yolk and the perivitelline space visible. For mature females the length of the apparent largest oocyte was estimated to the nearest 0.1 mm using an ocular micrometer.

To determine oocyte size frequency of mature females, a portion of the ovary was teased apart on a glass slide, placed under a compound microscope at 100×, and the lengths of oocytes over 0.40 mm measured to the nearest 0.01 mm until 20-30 of the largest oocytes were measured. Spawned nehu eggs are ellipsoidal with the length about twice the width (Yamashita 1951). Oocytes >0.3-0.4 mm are also elongate but are more variable in shape. "Length" as used here refers to the maximum dimension. Extremely elongate (length to width ca. 3 or more) and nearly round (length to width less than ca. 1.5) oocytes were noted as was the relative opacity of each oocyte measured. These observations were necessary in many cases to separate nearly round, heavily yolked oocytes that belonged to an advanced mode from very elongate, more nearly translucent oocytes of the same "length" that clearly belonged with a less developed mode.

As reported by Leary et al. (1975), mature female nehu may carry 0-2 separate size-frequency modes of oocytes. If a distinct advanced mode of oocytes was evident from the measurements and associated notes, the maximum, minimum, and median lengths of oocytes in this "largest" mode were used for subsequent analyses. These parameters will be abbreviated as LMX, LMN, and LMD, respectively. If all ova in the most advanced mode were hydrated, all lengths were arbitrarily assigned a value of 1 mm. If the largest mode was incompletely separated from smaller oocytes, only LMX and an estimate of LMD were recorded; if there was no separating mode evident, LMX (the largest oocyte in the subsample) was the only datum recorded. If an advanced mode was present and a second or "next" mode was also separated from yet smaller oocytes; the maximum, minimum, and median lengths of oocytes in the next mode will be abbreviated NMX, NMN, and NMD. In most females, however, the next mode was either only partially separated or not evident and, similarly to the case for unseparated advanced modes, only NMX and an estimate of NMD or only NMX, the largest oocyte not in the advanced mode, could be recorded.

For 107 specimens for which size-frequency measurements were made from a sample of the right ovary, the left ovary was prepared, sectioned, and stained with eosin/hemotoxylin as described by Hunter and Goldberg (1980). The slides, identified by only a code number, were examined for presence of postovulatory follicles (POF).

For determination of batch fecundity and dry weight, the fish was first rinsed with distilled water. The ovaries were removed and placed on a clean glass slide. Oocyte size frequency was determined as described above. If a distinct mode of advanced oocytes was present and oocytes in this mode could

be unequivocally discriminated under a dissecting microscope on the basis of size or opacity, the ovaries were teased apart and all ova in the advanced mode counted. This technique eliminated any error in fecundity determination due to subsampling of the ovaries, but meant that very few determinations were based on specimens with oocytes smaller than ca. 0.65 mm. In most of the latter cases, even if an advanced mode was clearly evident from the size-frequency determinations, it could not be unequivocally discriminated for total counts under the dissecting scope. Females with hydrated ova free from the follicles and segregated from the smaller oocytes were not used for fecundity determinations.

After the oocytes in the largest mode were counted, the entire ovaries were rinsed with distilled water from the slide into a preweighed aluminum pan. The stomach contents were removed from the fish and the body cavity was examined for parasites, specifically the presence of ca. 5 mm long nematodes around the liver and pyloric caeca. The fish was placed in a preweighed pan, and any tissue remaining on the slide was rinsed with distilled water into the same pan. The fish and gonads were dried at 60°C for 24 h after which the pans were reweighed to the nearest 0.1 mg, and dry weights of the fish and gonads determined by subtraction.

In all cases, fecundity and relative fecundity refer strictly to batch fecundity. Relative fecundity will be given as eggs per gram ovary-free dry weight, and gonad to somatic weight ratio (G/S) will be given as percent of dry weight values. Dry weights were used because of the difficulty in making consistent wet weight determinations on such small fish and even smaller ovaries. Careful wet-dry weight determinations on 10 females and gonads indicated that preserved nehu without gonads are about 73% water and that ovaries with yolked, but unhydrated, oocytes are about 60% water. To compare nehu fecundity data with those from other studies which had used wet weights, individual nehu dry weights were divided by 0.27, and relative fecundity and fecundity weight relationships were recalculated. This procedure admittedly ignored any variability in the wet-dry weight relationship. The G/S values given here can be multiplied by 0.675 (0.27/0.40) to make them roughly comparable to values based on wet weight from other studies.

Unless otherwise noted, all regressions given below are Model II (or "functional"), GM regressions (Ricker 1973). Results of regressions using natural logarithms are expressed as power curves (antilog form). The 95% confidence limits for slopes of linear regressions and exponents of power curves (= slopes of ln-ln regressions) were calculated from formulae in Ricker (1975). For any previous studies which had given results from Model I regressions, original fecundity and weight data were used to calculate functional regressions.

RESULTS

Maturity and Oocyte Development

The smallest mature females were 35 mm SL, the same minimum size reported by Leary et al. (1975), but in many of the samples most of the fish <40 mm SL were immature. Among the fish from the 36 samples from which more than cursory examinations were made, 30% of the 134 specimens <40 mm SL were immature. Only 8% of the 227 between 41 and 45 mm SL and <2% of the 284 over 45 mm were immature.

Nehu oocytes begin to elongate at about 0.3 mm in length but remain relatively translucent with little visual evidence of vitellogenesis until about 0.4 mm long. Oocytes longer than 0.5 mm were almost always opaque, and those over about 0.6 mm were densely opaque and yellow to yellow-brown in color. The first signs of hydration appeared in oocytes about 0.75 mm long. The yolk became more translucent and globular rather than granular in apparent texture, and the perivitelline space was evident at one or both ends. All ova longer than 0.8 mm were white in appearance and had an evident perivitelline space. At about this size or slightly larger, ova had left the follicles and begun moving to the main oviduct. Comparisons of fish from closely spaced purse seine samples taken just before and during spawning indicated that migration of hydrated ova from the follicles to the oviduct occurred in <0.5 h. Only in a few fish with the ova segregated or partially spawned were one or two hydrated ova left in the follicles. Apparently once hydration begins, all ova in a batch are normally ovulated and spawned at one time.

Separate batches of maturing oocytes become distinct from the numerous small oocytes between 0.45 and ca. 0.60 mm. In fish with LMX <0.45-0.50 mm there was little or no evidence of a separating size-frequency mode of oocytes. Variably separated modes with LMD at 0.45-0.55 mm were present in fish with the LMX at 0.55-0.65 mm. Usually modes centered at 0.60 mm or larger and with LMX over 0.65 mm were clearly separated from smaller and less opaque oocytes. There was no evidence from size-frequency data that, once oocytes reached ca.

0.65-0.70 mm long, any were "left behind" and not spawned with the ripening batch.

For 248 fish which either had a clearly defined and separated advanced mode of unhydrated oocytes or carried hydrated ova with a clearly defined and separated next mode, the largest (LMX or NMX) and median-sized (LMD or NMD) oocyte in the mode were significantly correlated ($r = 0.94$, $P < 0.01$), and the slope of the Model II regression was nearly 1 (1.042). The correlation was essentially unchanged by addition of data from 51 more fish where the median size of an incompletely separated mode was only estimated. These results indicate that, even if a mode is incompletely separated, the estimated LMD is a useful parameter and, furthermore, that for purposes of comparing different fish, LMX is as appropriate an indicator of size of oocytes in a mode as LMD. Consequently, in subsequent analyses of LMD data both unequivocal and estimated values were used, and in other cases LMX was used to analyze change in oocyte size during ripening. Both decisions were made primarily to include data from specimens with small oocytes and without completely or even partially separated modes.

Fecundity

Fecundity of 222 females 35-58 mm SL ranged from <100 to >1,600, and relative fecundity ranged from 432 to 4,098 eggs/gram. Although low relative fecundities were observed in samples from almost all months, most values over 2,000 were from fish taken in summer and fall (Fig. 1); consequently, the fecundity data from "winter" (November through April) and "summer" (May through October) fish were treated separately for all subsequent analyses. There were no significant differences in size composition between the summer and winter specimens (Kolmogorov-Smirnov test, $P > 0.20$). The mean relative fecundity for winter (1,363, $n = 93$, range = 496-2,763) was significantly different ($P < 0.01$, t-test) from that for summer (2,097, $n = 128$, range = 433-4,099). Regressions between fecundity and length or weight (Table 1) also indicated that winter fish were less fecund than summer fish.

When relative fecundity data for each season were partitioned according to LMD (<0.65 mm, 0.65-0.75 mm, and >0.75 mm), there were no significant differences between groups in the summer data (analysis of variance, $P > 0.05$), but there were significant differences in the winter data ($P < 0.001$). Inspection of the data indicated that the latter was due mostly to low values for the fish with LMD <0.65 mm. This could result from incomplete recruitment of oocytes to modes barely separated from smaller oocytes. There were, however, only 12 fish in this category, and the small sample size plus the absence of similar evidence in summer fish indicates

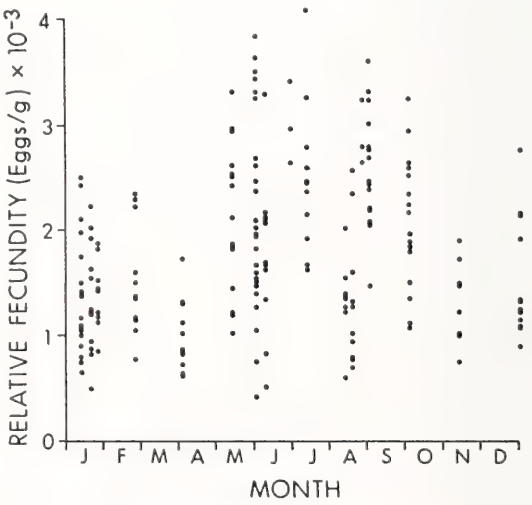

FIGURE 1.—Relative fecundity in thousands of eggs/g ovary-free dry weight vs. date of collection for 222 nehu from Kaneohe Bay, HI.

TABLE 1.—Summary of Model II regression statistics for relationships between length and weight and between fecundity and size based on data from 128 "summer" and 94 "winter" nehu plus relationship between gonad weight and bodily weight for 67 summer and 44 winter nehu with hydrated ova. Variables are standard length in mm (SL), ovary-free bodily dry weight (S) and total dry ovary weight (G) in g, and fecundity in numbers of ova in the most advanced mode (F). Results of regressions based on natural logarithms are given as power curves (antilog form). The 95% confidence limits are given for either the slopes of linear equations or the exponents of power curves.

X,Y	Summer	(95% CL)	r^2	Winter	(95% CL)	r^2
ln SL, ln S	$S = 8.868 \times 10^{-7}\ SL^{3.25}$	(3.11-3.40)	0.94	$S = 3.696 \times 10^{-7}\ SL^{3.47}$	(3.30-3.65)	0.94
SL, F	$F = -2352 + 63.1\ SL$	(56.3-70.6)	0.59	$F = -1465 + 38.9\ SL$	(33.6-45.0)	0.51
ln SL, ln F	$F = 6.073 \times 10^{-8}\ SL^{5.95}$	(5.24-6.75)	0.49	$F = 1.226 \times 10^{-8}\ SL^{6.24}$	(5.45-7.15)	0.56
S, F	$F = -351 + 3787\ S$	(3,420-4,194)	0.66	$F = -223 + 2444\ S$	(2,119-2,819)	0.53
ln S, ln F	$F = 7094\ S^{1.83}$	(1.63-2.05)	0.56	$F = 4{,}538\ S^{1.80}$	(1.57-2.05)	0.59
ln S, ln G	$G = 0.2339\ S^{1.88}$	(1.65-2.14)	0.72	$G = 0.1192\ S^{1.61}$	(1.32-1.95)	0.60

that the significant differences for winter may have resulted from chance alone.

The regression statistics (Table 1) for data from each season indicate a great deal of variability about the functional relationships between fecundity and length or weight or between the logarithms of these. The correlation coefficients (r) for all regressions were significantly ($P < 0.05$) different from zero, but the coefficients of determination (r^2) indicated that only about half the variance of fecundity or ln fecundity was accounted for by the regression. The exponents from the logarithmic regressions of fecundity on length are considerably higher than those of the weight-length relationships, and the exponents from the logarithmic regressions of fecundity on weight are significantly greater than one. Both indicate that fecundity is not linear with weight and that the appropriate expressions for the functional relationship with size are the power curves for fecundity vs. weight. The exponents of the curves for the two seasons were nearly the same, while the summer-winter ratio of the preexponential factors (antilogs of the regression intercepts), 1.56, was almost identical with the ratio of mean relative fecundities, 1.54.

A small, but significant part of the variability in fecundity within seasons was related to variation in length-weight relationships of the fish. Using predictions of weight and fecundity from Model I (least squares) logarithmic regressions on standard length, I tested for correlations between relative deviations (observed-predicted/predicted) of fecundity and weight. The relative deviations were positively and significantly correlated for both seasons (summer: $r = 0.44$, $P < 0.01$; winter : $r = 0.24$, $P < 0.05$). The coefficients of determination, however, indicate that the variation in relative deviation from predicted weight accounted for small percentages of the variation in deviation from predicted fecundity. Maximum relative deviations in weight were ca. $\pm 20\%$ about the predicted value, while deviations in fecundity were much broader: $\pm 75\%$ in summer and $\pm 60\%$ in winter. Thus there was a tendency for relatively "fat" individuals to have higher fecundity, but this did not account for much of the scatter in the fecundity data.

Nematodes were the only parasites noted frequently, and their presence had a minor and insignificant effect on fecundity. About half of the summer fish and about a third of the winter fish had nematodes. For both seasons, the exponent from the logarithmic regression of fecundity on weight was higher for fish without nematodes than for those with them, but the 95% confidence limits overlapped.

G/S values ranged from under 2% to about 12% in summer fish and to about 7% in winter fish. For females with maturing oocytes, G/S is a function of both the number and size of oocytes. LeCluse (1979) showed for *Sardinops ocellata* that ovum dry weight does not increase once hydration begins, and my own preliminary data indicated that this was also true for nehu. Thus effects of variation in oocyte size could be eliminated by considering only fish with LMD >0.75 mm—the size at which hydration begins. The mean G/S for such fish from winter was 4.8% ($n = 67$: range: 2.4-7.1%) and from summer, 6.3% ($n = 44$; range: 2.1-12.0%). Among fish with LMD >0.75 mm, the exponents from logarithmic regressions of gonad weight on fish weight were significantly greater than one for both seasonal groups (Table 1).

Postovulatory Follicle Deterioration

Although the number of specimens examined for postovulatory follicles (POF) was limited (107 from 13 different samples), the results indicated that POF were a reliable indicator of recent spawning up to about 16 h after spawning. Among the 80 specimens from 9 samples taken 1-5 h after estimated spawning time, follicles were either present and obvious or completely absent. Only seven mature females were available from between midnight and dawn. There were no traces of POF in one specimen; in the others, POF were obvious but showed some signs of degradation similar to that described for northern anchovy, *Engraulis mordax*, by Hunter and Goldberg (1980). Among the 20 specimens from two samples taken 14-16 h after spawning, POF were further degraded but still distinguishable from other structures in half the fish, while the others showed no traces. Judged from descriptions of POF in *E. mordax* by Hunter and Goldberg, 14-16 h in nehu appears roughly equivalent to 24 h in *E. mordax*. Although controlled experiments such as those of Hunter and Goldberg were not conducted, it seems likely that, later in the day, POF cannot be distinguished reliably enough to indicate spawning the previous night. Since POF were either present and very obvious or totally absent in fish collected during the night, all traces of previous spawning are apparently gone after about 24 h.

Spawning

Examination of fish from purse seine samples

taken over deep water after sunset indicated that spawning began and ended during a relatively brief period near the predicted spawning time and that most females in the early night samples were spawners. Ten samples were taken within ±40 min of the predicted spawning time. In four of these, 96-100% of the mature females in each (a total of 85 examined) carried hydrated ova. Most of those with hydrated ova appeared to have not yet started to spawn, i.e., the hydrated ova were not completely separated from the ovarian tissue and smaller oocytes. In the other six samples, 0-75% of the females (total = 114) carried hydrated ova; most of these appeared to be either partially or nearly completely spent. The largest oocytes in those with no hydrated ova were usually <0.65 mm—about the same size as the largest unhydrated oocytes in those with some hydrated ova present. Only 17 of the specimens without hydrated ova were examined histologically; POF were present in 13. Although it is not possible to separate spawners from nonspawners unequivocally on the basis of oocyte size (see below), the small size of the oocytes and the high fraction with POF among those examined indicate that most of the fish without hydrated ova from these samples had just finished spawning.

Later in the night, the frequency of females with hydrated ova decreased, and nonspawning fish appeared to occur more frequently. In 16 samples taken between 40 min and 2 h after predicted spawning time the percentage of females that carried hydrated ova ranged from 0 to 80%. Most values were <25%, and only 24% of total of 332 examined carried hydrated ova. Most of those with hydrated ova appeared at least partially spent; many carried only a few at the posterior end of the oviducts. In 14 of these samples, most of the females without hydrated ova were probably recent spawners. The largest oocytes present were <0.65 mm long, and POF were present in 19 of 20 fish examined histologically. In two other samples, however, several of the females carried larger unhydrated oocytes; POF were present in only 6 of 10 examined from one of these samples. Among the 20 samples taken later in the night (2-4 h after predicted spawning time), only 5 of 254 mature females carried hydrated ova, and oocytes >0.65 mm were present in many of the others. POF were present in only 10 of 20 females examined from two of these samples.

Spawning Frequency and Oocyte Development Rate

Oocyte size-frequency data for 135 fish taken between 0 and 3.25 h after spawning time indicated that spawners carried smaller oocytes than nonspawners. Few of these fish had clearly defined modes of unhydrated oocytes, so LMX (or NMX if hydrated ova were present) was used as a measure of oocyte development. The 20 specimens without POF carried significantly larger oocytes than those with either POF or some hydrated ova present (Table 2). Although there was some overlap in the size ranges of the two groups (Fig. 2), most of the other fish taken during this period but not examined histologically had relatively small oocytes and were probably recent spawners.

Oocyte size-frequency data from fish taken inshore in the morning, 14-16 h after last spawning time,

TABLE 2.—Means and ranges of largest oocyte in the most advanced (first) or next mode of oocytes for nehu taken over spawning areas at night and in shallow areas during the morning and afternoon. For night fish which had some hydrated ova present, the datum used was the largest unhydrated oocyte. Collection times were adjusted to hours since estimated time of the most recent spawning. For night and morning, "S" indicates fish that spawned the night of or the night before collection; for afternoon, "S" indicates fish about to spawn the next night. Similarly, "NS" indicates fish that had not spawned the night of or before collection or were not about to spawn the next night. Probability values between three pairs are based on *t*-tests.

Time	Hours since spawning time	Group	*N*	Mode	Largest oocyte (mm) Mean	(Range)	
Night	0-3.25	S	115	First or next	0.56	(0.46-0.71)	$P < 0.001$
	0-3.25	NS	20	First	0.66	(0.50-0.72)	
Morning	14-16	S	10	First	0.64	(0.60-0.70)	$P < 0.001$
	14-16	NS	10	First	0.72	(0.69-0.75)	
Afternoon	20-24	S	59	Next	0.52	(0.42-0.63)	$P < 0.001$
	20-24	NS	45	First	0.68	(0.60-0.75)	

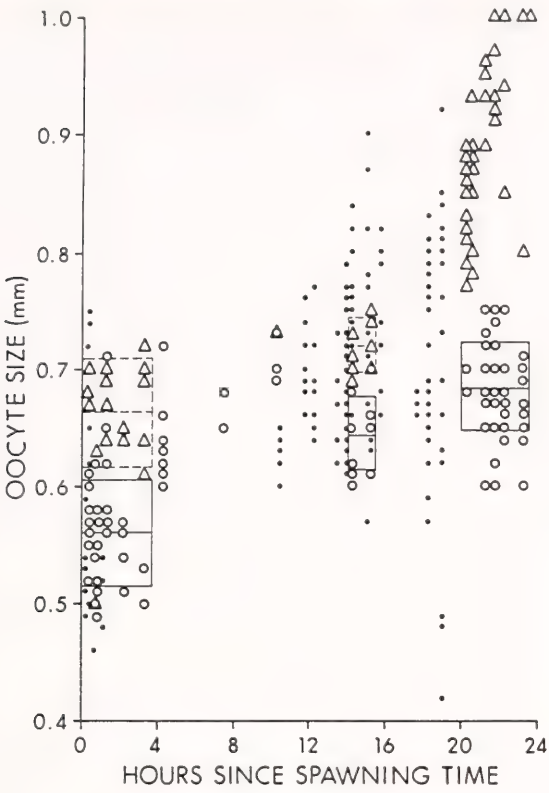

FIGURE 2.—Maximum oocyte size vs. estimated hours since the most recent spawning time for 460 nehu collected at different times of the day from Kaneohe Bay, HI. Large open circles represent fish that either were spawning or had spawned at or near 0 hours (i.e., the night of or the night before collection) or were unlikely to spawn at 24 h (i.e., the next night). For such fish taken 0-3 h after estimated spawning time, the data points indicate the largest unhydrated oocyte. Triangles represent fish that had not spawned at 0 h or were apparently going to spawn at 24 h. Small solid circles represent fish which were not examined for postovulatory follicles and could not be assigned to the above groups on the basis of oocyte size alone. Solid and dashed lines indicate the mean and ±1 standard deviation of maximum oocyte size (horizontal lines) for fish represented by circles and triangles, respectively, for three different time intervals (vertical lines) considered in Table 2.

indicated that oocyte size of both spawners and nonspawners had increased considerably over nighttime values. The LMX of the 10 specimens without POF averaged significantly higher than that of the 10 with POF (Table 2). The mean LMX for spawners had increased to almost the same value observed for nonspawners in the night samples, while that for nonspawners was almost at the size at which hydration begins. Other fish taken at the same times, but not examined histologically, already carried some hydrated ova (Fig. 2).

Data from later in the day indicated that the previous night's nonspawning fish do in fact begin hydrating ova and eventually become the spawners of the next night. Hydrated or hydrating ova occurred in about half the fish taken inshore between 16 and 24 h after last spawning, and most of the rest of the fish had considerably smaller oocytes (Fig. 2). In 67 of 138 specimens taken inshore more than 20 h after the last spawning time (and thus 4 h before the next spawning time), the largest mode was clearly separated from smaller oocytes; LMX was >0.75 mm; and at least some ova were hydrated. The NMX of 59 fish in this group averaged slightly but significantly (t-test, $P > 0.001$) smaller than the largest unhydrated oocytes of spawning fish from offshore early night samples (Table 2, line 5 vs. line 1). This indicates that during hydration and spawning of the current batch, which require no further increase in dry weight or energy content, the oocytes in the next batch were already starting to advance toward the next spawning.

Although some of the remaining fish in the late afternoon (+20 h) samples could conceivably have begun hydrating oocytes and spawned by evening, most appeared to be spawning fish from the night before that were to become the nonspawners of the next night. LMX was >0.70 mm in only 9 of the 71 fish in this group, and about 25% of the 45 examined for oocyte size frequency did not have a clearly separated mode. The mean LMX of these 45 fish did not differ significantly ($P > 0.05$) from that of the nonspawners from the early night samples (Table 2, line 6 vs. line 2). The LMX did, however, average significantly ($P < 0.005$) higher than that of the previous night's spawners in the morning samples (Table 2, line 6 vs. line 3), thus indicating continued oocyte growth between morning and late afternoon.

In summary, the data indicate that most mature female nehu spawn every other day. The largest oocytes present just after spawning increase substantially in size by the next morning and appear to reach the size found in nonspawning night fish by late afternoon. The largest oocytes in nonspawning fish at night are almost at the point where hydration begins by morning, and appear to begin hydrating then or shortly afterwards such that the previous night's nonspawners are nearly ready to spawn by late afternoon.

Alternative cycles are either impossible or difficult to reconcile with the data. If spawning were more frequent, i.e., every day, there would be no nonspawners. This was essentially the case in most night samples taken over the spawning areas, but the day samples averaged about 50% spawners as would result from an every other day cycle. Less

frequent spawning is not consonant with the apparent growth of oocytes in the 24 h after spawning and the near absence of fish with LMX <0.60 mm in the late afternoon samples. Some individuals may, however, spawn more or less frequently than every other day. In the early night samples, some spawners carried larger oocytes than most nonspawners and some of the latter carried smaller oocytes than most of the former (Fig. 2). Thus a few spawners appeared to be capable of ripening the next batch in 24 h rather than 48 h, and the largest oocytes of some nonspawners appeared unlikely to be ready for spawning within 24 h.

DISCUSSION

Results of the present study indicate that the rate of oocyte development in nehu is much faster than in the northern anchovy, *Engraulis mordax*, or the Peruvian anchovy, *E. ringens*, the only other species for which comparable data are available. Hunter and Goldberg (1980) showed that oocytes of *E. mordax* which had spawned within 24 h averaged 0.46 mm long and, during the peak spawning season, grew to the size at which hydration begins in about 7 days. Alheit et al. (1984) indicated that about 6 d are required in *E. ringens*. In nehu, oocytes in largest mode just after spawning averaged 0.52 mm (mean LMD of 54 spawners taken within 3 h after spawning); these appear to advance to hydration stage in <48 h. Hunter and Goldberg's results also indicated that about 7% of the oocytes in the largest mode are not hydrated and spawned; whereas, in nehu it appears that once a batch of oocytes is separated from smaller oocytes, oocytes in that batch are rarely left behind and not spawned with majority of the batch.

Hydration, spawning, and degeneration of POF after spawning are also more rapid in nehu than in the *Engraulis* species. In *E. mordax* hydration begins in the morning about 12 h before spawning begins (Hunter and Macewicz 1980); Alheit et al.'s (1984) data indicated that *E. ringens* is similar. Both studies indicated that the *Engraulis* species spawn over a broad period after sunset with peak spawning just before or near midnight. Nehu ova to be spawned on a given night begin hydrating only a few hours before spawning, and spawning occurs over a rather brief period shortly after sunset. Whereas POF are reliably identifiable up to 24 h after spawning in *E. mordax* and even longer in *E. ringens* (Hunter and Goldberg 1980; Alheit et al. 1984), they appear to degenerate to a similar point in about 16 h in nehu.

My estimates of spawning timing and duration conflict with those of Yamashita (1951) upon which Tester (1955) apparently based his statements that nehu spawn around midnight. As mentioned earlier, studies in progress on appearance of newly spawned eggs confirm the pattern indicated by presence of females with hydrated ova in purse seine samples after sunset. These studies further indicate that Yamashita was probably not sampling deep enough in the water column to collect newly spawned eggs and that his "freshest" eggs were actually one or more hours old.

One of the broader implications of this study is that, when dealing with tropical species, the time scale of sampling must be on the order of hours rather than weeks or days. The latter may be appropriate for investigation of species from higher latitudes, but would miss many events or stages in the reproductive cycle of nehu. Leary et al.'s (1975) conclusion that nehu spawn only once per lifetime was in part based on the rarity of females with hydrated ova in their samples. This was almost certainly due to their not sampling during the short period between late afternoon and shortly after sunset when hydrated ova are found in the current night's spawners. Leary et al. stated that all females with hydrated ova were captured between 2100 and 2300 h, i.e., well after the peak of spawning even in summer.

Both of the above studies of *Engraulis* species indicate some degree of segregation of spawning females at or near spawning time; spawners tended to be overrepresented in such samples. Segregation appears more extreme in nehu; the purse seine samples taken just before and after spawning time were almost all spawners. The greater percentage of nonspawners in some purse seine samples taken later after spawning and the nearly 1:1 ratio of spawners to nonspawners in most day samples indicate that spawning fish remix with others later during the night and that segregation of the next night's spawners does not occur until the mixed schools leave shallow day areas at or near sunset. The distribution of nonspawners early in the night is not known.

The winter-summer differences in nehu fecundity were evident from both the comparison of relative fecundity and the regressions of fecundity on either length or weight. The G/S data for fish with ova >0.75 mm also showed a higher mean and broader range in summer. Other data (Clarke unpubl. data) indicate that spawned nehu eggs are about 20% heavier in winter, but this difference is insufficient to compensate for higher fecundity in summer fish.

The summer-winter ratio of mean relative fecundity was 1.54; roughly corrected for the egg weight difference, the ratio of mean effort per spawning would be 1.28 (1.54/1.20), about the same as the ratio of mean G/S, 1.31. There was no evidence that winter fish compensated for lower effort per spawning with higher frequency.

The causes and adaptive value of the much greater range and, on the average, higher effort by summer fish are not obvious. Similar differences have been reported between different populations of other species. For example, the northern population of *E. mordax* appears to be more fecund than the central population (Table 3). This difference is probably genetic and appears to reflect the shorter spawning season (and lower number of batches) in the northern population (Laroche and Richardson 1980). Since nehu live <6 mo (Struhsaker and Uchiyama 1976), it is difficult to postulate that the differences between summer and winter fish are genetic. It is, however, possible the winter fish may spawn for longer periods and thus to some degree compensate for lower effort per spawning.

The winter-summer differences in nehu reproductive effort per batch may simply be physiological consequences, perhaps with neutral or even negative adaptive value, which result from seasonal differences in the environment. If output in nehu is closely linked to recent feeding success (see below), the output could be lower in winter fish if average daily ration were lower. There is, however, no evidence of major seasonal differences in standing crop of the macrozooplankton upon which adult nehu feed (Hirota and Szyper 1976). Also, nehu feed almost exclusively at night (Clarke unpubl. obs.), and actually have a longer feeding period per diel cycle during the winter. Although the difference between summer maxima and winter minima of temperature in Kaneohe Bay is only about 5°C, it is possible that metabolic processes overall, and consequently both daily ration and reproductive output are slowed enough in winter to account for the observed difference.

Regardless of season, the relative fecundity data combined with minimal estimates of spawner abundance from purse seine catches predicts planktonic egg densities 2 or 3 orders of magnitude higher than those reported by egg surveys of Tester (1955) or Watson and Leis (1974). Assuming all fish in a ca. 300 m^2 area were captured, catches of several purse seine sets indicated 0.3-0.5 g dry weight of spawning females/m^2 and predicted egg densities of 10^2-10^3/m^2. Studies in progress have shown that such egg densities do in fact occur routinely, but that most of the eggs are deeper than 5 m in the water column. Thus the earlier egg surveys, which used surface plankton tows, had missed over 90% of the spawned eggs.

Comparable fecundity data are available for only a few other species of anchovies (Table 3), and most

TABLE 3.—Fecundity-weight relationships for winter and summer nehu, *Encrasicholina purpurea*, and five other species of anchovies. Means and standard deviations of relative fecundity and power curves for fecundity vs. weight were calculated from available fecundity and weight data. Fish weight were ovary-free wet weights except for nehu, whose wet weights were estimated from dry ovary-free weight data, and *Engraulis ringens*, for which the data were given as total fish wet weight. Power curves are the antilog forms of equations based on Model II linear regressions of the natural logarithms; 95% confidence limits are for the exponents. Relative fecundities of the smallest and largest female from each group were calculated from the extremes of weight values and the appropriate power curve.

Species	*N*	Fish weights (g)	Relative fecundity (eggs/g) Mean (+2 SD), smallest-largest		Fecundity vs. weight (95% C.L.)	Reference
Encrasicholina purpurea						
Summer	128	0.4-1.8	566 (±436),	284-1,043	$F = 647\ W^{1.83}$ (1.63-2.05)	This study
Winter	94	0.4-1.3	368 (±266),	195-542	$F = 431\ W^{1.80}$ (1.57-2.05)	This study
Engraulis mordax						
Central	67	9.3-31.9	421 (±295),	261-561	$F = 65.6\ W^{1.62}$ (1.36-1.93)	Hunter and Macewicz 1980
North	21	14.4-31.3	826 (±449),	650-1,094	$F = 108.9\ W^{1.67}$ (1.19-2.34)	Laroche and Richardson 1980
Engraulis ringens	83	11.8-41.5	651 (±404),	493-709	$F = 241\ W^{1.29}$ (1.09-1.53)	Miñano 1968
Cetengraulis mysticetus	86	24.5-69.5	863 (±529),	613-1,233	$F = 71.9\ W^{1.67}$ (1.45-1.93)	Peterson 1961
Stolephorus heterolobus	9	1.6-6.3	469 (±173),	410-514	$F = 379.4\ W^{1.165}$ (0.89-1.53)	Muller 1976
Anchoa naso	12	0.8-5.6	885 (±672),	1,257-618	$F = 1,159\ W^{0.64}$ (0.43-0.94)	Joseph 1963

of these species are much larger than nehu. The reproductive size range of nehu overlaps slightly with only *Stolephorus heterolobus* and *Anchoa naso*. Unfortunately, previous studies of these two species involved very few specimens, and the summary statistics must be regarded as less reliable than those of the other species in Table 3.

Mean relative fecundities for nehu appear to be lower than those of most species; however, the usefulness of this parameter is questionable because the exponents of the power curves relating fecundity and weight are considerably (and significantly) greater than one in most of the species. Thus mean relative fecundity, a commonly used comparator, would be affected by the size range and size composition of the sample of females upon which fecundity and weight are based. When two groups of similar size composition are compared, as in the case of summer and winter nehu, the difference in mean relative fecundity is similar to that indicated by comparison of power curves, but otherwise, such as when comparing different-sized species, mean relative fecundities are likely to give erroneous or at best misleading results. Mean relative fecundity also ignores the differences between small and large individuals of the same species or population.

The exponents of the power curves for nehu are considerably higher than those of any other species. Although the 95% confidence limits for these values do not exclude those for all the other populations, this indicates that the rate of increase in relative reproductive output with increasing size is greatest in nehu. The consequences are illustrated by the relative fecundities calculated for the smallest and largest fish of each population using the power curve for that species (Table 3). Relative fecundities of the largest females are 1.2-2.2 times those of the smallest in the other species but 2.8 and 3.7 times greater in winter and summer nehu, respectively. Both the smallest and largest winter nehu appear to be less fecund per unit weight than the smallest and largest females of all or most of the other species. Small summer nehu also have considerably lower relative fecundity than most of the others, but the value for large summer nehu is among the highest. Ignoring the rather questionable results for *Anchoa naso* (only 12 individuals), the value for the largest *Cetengraulis mysticetus* is the only one substantially greater than that of the largest summer nehu.

Although these comparisons must be regarded as tentative because many between-species differences in power curve exponents are not significant, nehu seem to be distinguished from other anchovies not by differences in relative fecundity but rather by differences in the relation between relative fecundity and size. Speculation about the possible relation of this to differences in environment and other life history parameters, such as nehu's short life span and maturity soon after metamorphosis, is unwarranted without evidence that similar differences exist between large and small species in other taxa. Nevertheless, it seems possible that the pattern of allocation of resources between growth and reproduction over the reproductive life span is yet another life history parameter which could be selected for by prevailing adult mortality rates, predictability of larval survival, etc.

Comparison of fecundities alone does not adequately reflect differences in reproductive effort if there are differences in egg size. For example, nehu eggs average about two-thirds the egg weights calculated for *E. mordax* by Hunter and Leong (1981). Effort per batch would be best measured by relative cost in terms of dry weight, calories, etc., rather than numbers of eggs. Available data permit only crude comparisons of the two species.

The intercept of the regression equation for G/S vs. fecundity of nehu with ova >0.75 mm is about 2.5% for fish from both seasons and nearly the same as the mean G/S (2.4%) of 21 other fish whose largest oocytes were 0.48-0.65 mm and had presumably just spawned. (G/S data were not available for fish used for POF analyses.) Using 2.5% as the mean G/S 2 days before spawning and subtracting this from mean G/S of nehu with ova >0.75 mm, i.e., those about to spawn, gives mean relative weights per batch of 3.8% of bodily dry weight in summer and 2.3% in winter. These estimated relative costs per batch are minimal since they do not include investment in bringing oocytes to the size at 2 days before spawning.

Hunter and Leong (1981) did not give relative cost per spawning of *E. mordax* in terms of dry weight, but data in their table 4 plus an assumption of dry bodily weight equal to 25% of wet weight yield an estimate of about 4.4% of bodily weight per spawning for an average female. Hunter and Leong's data in table 1 indicated that dry weight in *E. mordax* declined about 30% during the main spawning season due to loss of fat; this loss is shown to be equal to the calories required for about 13 spawnings. If this is also true for dry weight then the loss per batch would be about 2.3% of dry bodily weight.

The above estimates of cost per batch in terms of dry weight are very crude and only indicate that nehu, particularly summer nehu, are probably similar to *E. mordax*. Additionally it is clear that nehu, like *E. mordax*, lose half or more of their ovary

weight with each spawning and must depend on bodily reserves and assimilation of food, rather than ovarian reserves, to continue spawning. As mentioned above, Hunter and Leong (1981) showed that about 65% of the caloric cost of spawning is supplied by fat reserves. Even if the same were true for nehu, the additional requirements for continued spawning would have to come from food assimilated and available for reproductive processes over a period of only 2 d rather than 7 d in *E. mordax*. Assuming cost per batch is 4% of dry bodily weight and that 65% of this comes from bodily reserves in both *E. mordax* and summer nehu, the average additional requirements per day would be 0.2% and 0.7%, respectively.

The above suggests that all aspects of reproductive output in nehu—batch fecundity, spawning frequency, and duration of spawning—would be very sensitive to any factors affecting availability of resources for reproduction. Parasite load, which has been shown to affect batch fecundity in cod (Hislop and Shanks 1981), apparently has only an insignificant effect on nehu, but since a batch is formed only 2 or 3 days before spawning and the ova to be spawned on a given evening do not attain maximum size until just a few hours before spawning, even recent events could affect the number or the growth rate of oocytes in a batch. Some of the great variation in fecundity and the indications that some fish spawn more or less often than normal could result from individual differences in recent feeding success, injury or stress from predators or the fishery, or perhaps the extent of inshore-offshore movements over the diel cycle. Unfortunately, none of these putative factors (except for serious injury) would leave any detectable trace on individual fish that might explain why fecundity or spawning frequency was higher or lower than average.

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ON THE COMPATIBILITY OF A NEW EXPRESSION FOR GROSS CONVERSION EFFICIENCY WITH THE VON BERTALANFFY GROWTH EQUATION[1]

Gross food conversion efficiency (K_1) is defined by

$$K_1 = \text{growth increment/food ingested} \quad (1)$$

$$= \frac{dW}{dt}/I$$

where I is the ingestion rate (Ivlev 1939; Ricker 1966); data from feeding experiments are usually fit to an allometric model of the form

$$K_1 = c\ W^{\alpha} \quad (2)$$

where W is the body weight, and c and α are empirical constants which, however, have the disadvantage of always predicting values of $K_1 > 0$, although the fish and other aquatic animals to which the model is meant to apply usually experience size constraints and hence must reach a value of W where $K_1 = 0$. It is therefore preferable to choose a functional form for K_1 which falls to zero as W approaches W_∞. Furthermore, recent analysis of feeding studies of a number of fish species indicates that K_1 can approach arbitrarily close to unity for the smallest fishes, which suggests the alternate equation

$$K_1 = 1 - (W/W_\infty)^{\beta} \quad (3)$$

where W_∞ is the weight at which $K_1 = 0$, and β is an empirical constant estimated from the slope of

$$\log (1 - K_1) = \beta \log W - \beta \log W_\infty \quad (4)$$

(Pauly 1986).

In this note we show that Equation (3) is compatible with the von Bertalanffy growth function (VBGF), both in its standard (von Bertalanffy 1938) and generalized forms (Richards 1959; Pauly 1981), which is not true of Equation (2).

We assume that the ingestion rate (I) can be expressed as an allometric expression of weight of the form

$$I = HW^d, \quad (5)$$

where H and d are empirical constants. From Equation (1) we then obtain for the growth rate

$$dW/dt = K_1\ HW^d \quad (6)$$

which combined with Equation (3) gives

$$dW/dt = (1 - (W/W_\infty)^{\beta})\ HW^d \quad (7)$$

and hence

$$dW/dt = \mathrm{HW}^d - kW^m \quad (8)$$

where $m = d + \beta$ and $k = H/W_\infty^{\beta}$. Equation (8) is the differential form of the VBGF, and can be integrated for various values of the constants m and d. Setting $d = 2/3$ and $m = 1$ (i.e., $\beta = 1/3$) yields the "normal" VBGF for weight,

$$W_t = W_\infty (1 - e^{-K(t-t_0)})^3 \quad (9)$$

where $K = k/3$, while if $m = 1$ and $0 < d < 1$ we get the generalized VBGF sensu Pauly (1981),

$$W_t = W_\infty (1 - e^{-KD(t-t_0)})^{3/D} \quad (10)$$

where $D = 3(1 - d)$. This second form is probably more useful as it allows for the exponent of the allometric relationship linking ingestion and weight (Equation (5)) to take wider range of values, as needed to fit various data sets and/or to mimic various models in the literature (see, e.g., Paloheimo and Dickie 1966 or Ursin et al. 1985).

The compatibility shown here between the recently proposed Equation (3) expressing K_1 as a function of fish weight and the VBGF is encouraging, as it supports the method suggested by Pauly (1986) for combining these two equations when estimating the food consumption of fish populations and leads to a mathematically consistent approach for the analysis of feeding and growth data.

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EFFECT OF A RIVER-DOMINATED ESTUARY ON THE PREVALENCE OF *CARCINONEMERTES ERRANS*, AN EGG PREDATOR OF THE DUNGENESS CRAB, *CANCER MAGISTER*

Carcinonemertes errans is a host-specific nemertean that can destroy large numbers of Dungeness crab, *Cancer magister*, eggs (Wickham 1979, 1980). Although the ectosymbiotic nemertean is present on adult and juvenile crabs of both sexes, its only known detrimental effect is to the egg stage. Wickham (1979) estimated that the direct mortality to eggs of Dungeness crabs off central California was 55%. High egg mortalities in the San Francisco, CA, area were suggested as a possible cause of the drastic decline in Dungeness crab populations in that area (Fisher and Wickham 1976; Wickham 1979).

From November 1983 through October 1985, the National Marine Fisheries Service (NMFS) conducted a comprehensive study of the distribution, abundance, and size-class structure of Dungeness crabs in the Columbia River estuary, a river-dominated estuary. Limited sampling was also done in adjacent coastal areas. As an incidental part of the study, we examined crabs for *C. errans*, and observed an effect of the river-dominated estuarine environment on the prevalence of *C. errans* on Dungeness crabs.

Methods

The study was done in the lower Columbia River estuary and adjacent coastal areas (Fig. 1). The estuary is a drowned river mouth that is dominated by river flows. Highest flows typically occur during the spring and lowest flows during late summer and fall. Estimated river flows (monthly averages) during the study period ranged from 3,121 m^3/s (August 1985) to 14,091 m^3/s (May 1985) (U.S. Geological Survey, Portland, OR). Salinities fluctuate widely in the estuary depending on river flow, tidal stage, and distance from the river mouth (Neal 1972). Inversely related to river flows, the salinity intrusion is typically least during spring and greatest during late summer and fall.

Sampling was done monthly at a maximum of 28 estuarine and ocean sites (Fig. 1). At 26 of the sites, an 8 m semiballoon shrimp trawl with stretched mesh size of 38.1 mm was used to collect samples; a 9.5 mm liner was inserted in the cod end of the net to prevent escape of small Dungeness crabs. Sampling in the estuary was normally done during times of higher salinity (early flood to early ebb tide).

Generally a subsample of at least 100 Dungeness crabs (≥20 mm) from each trawl effort was measured to the nearest mm (carapace width, anterior to the 10th anterolateral spines), weighed, sexed, and checked for eggs and *C. errans*. Specific body areas—the undersurface of the abdomen, the thoracic area covered by the abdomen, and the pleopods—were examined for *C. errans*. Dungeness crab catches at individual stations varied considerably, ranging from 0 to >100 crabs per trawl effort. Crabs <20 mm were measured and weighed, but were not routinely sexed or checked for *C. errans*.

Dungeness crabs were separated into four size classes: I (<50 mm), II (50-99 mm), III (100-129 mm), and IV (>129 mm). We used the chi-square test to compare the prevalences of *C. errans* on crabs in the ocean and the estuary and to compare the level of infestation between males and females within the two areas.

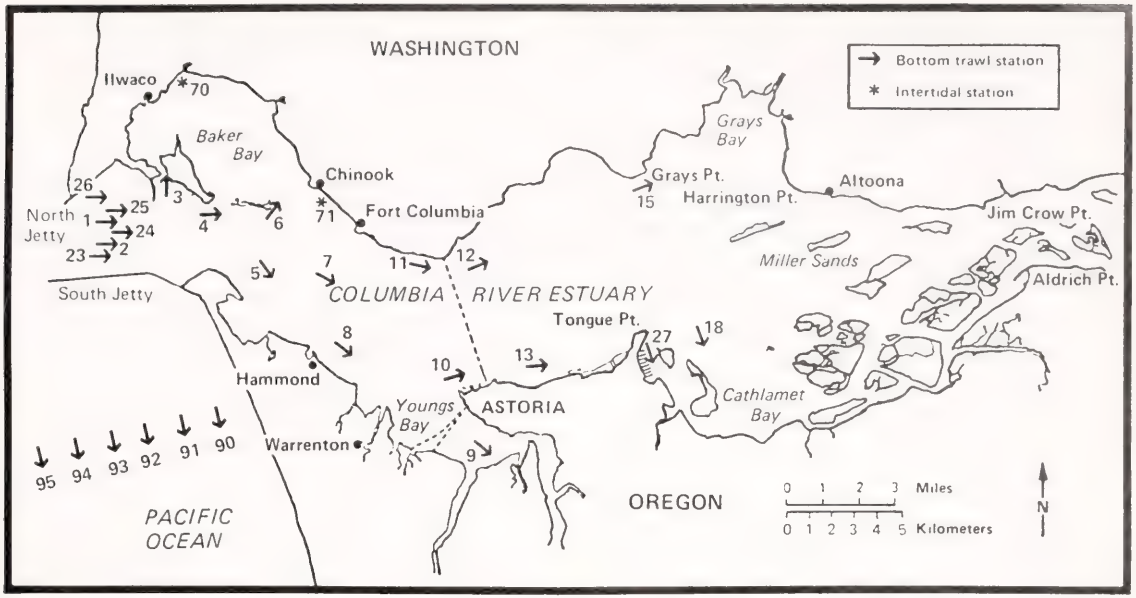

FIGURE 1.—Map of the Columbia River estuary and adjacent coastal areas, showing sampling sites for the 2-yr Dungeness crab study.

Results and Discussion

The prevalence of *C. errans* on Dungeness crabs collected in the estuary was significantly lower than the prevalence on crabs in the ocean (χ^2, df = 1, $P < 0.001$); average prevalences in the estuary and ocean were 6 and 79%, respectively (Tables 1, 2). Within the estuary, mean prevalence was highest at the mouth (stations 1, 2, 23-26) where it averaged 25%. In the estuary, significantly more females (8%) were infested than were males (5%) (χ^2, df = 1, $P < 0.001$), but in the ocean there was no significant difference ($P > 0.05$) in prevalence on males (80%) and females (76%). Only three egg-bearing females were collected during the study; they were collected December 1984 at the mouth of the estuary and in the ocean. One egg-bearing female had an obvious *C. errans* infestation.

In both the estuary and ocean, size class I Dungeness crabs were least frequently infested. No chi-square comparison was done for this size class because of the small numbers of infested crabs. In addition, the total sample size of size class I crabs in the ocean was small (46 crabs). For the individual size classes II-IV, the prevalences of *C. errans* on crabs were significantly lower in the estuary than in the ocean (χ^2, df = 1, $P < 0.001$). In the estuary, the infestation by *C. errans* was highest in size class IV crabs (29%).

The prevalence of *C. errans* found on Dungeness crabs in the ocean and the Columbia River estuary was lower than the prevalence reported by Wickham (1980) in the Bodega Bay, CA, area; he reported that all nonegg-bearing crabs >20 mm carapace width were infested with *C. errans*. In our study, some light infestations may have been missed by not examining the entire exoskeletons of the Dungeness crabs.

The major result of our examinations for *C. errans* was discovering the large difference in infestation levels between the ocean (79%) and the estuary (6%). Low salinities in the estuary, particularly upstream from the mouth, probably were the major cause of the lower infestation. During low river flows (about 4,400 m^3/s), when salinity intrusion is greatest, minimum bottom salinities in most of the lower 22 km of the estuary generally range from 0.5 to 15 ppt, although maximum salinities are ≥30 ppt. During high river flows (about 8,800 m^3/s), minimum bottom salinities in much of the lower 22 km of the estuary may be zero (Jay 1984). Wickham[1] noted that "Pure fresh water will kill worms in 1-2 minutes depending on the worms' size." The lower prevalence in the estuary may have have little effect on the overall prevalence in the ocean. Noninfested Dungeness crabs migrating from the estuary could be infested in the ocean by larval worms (Wickham 1980), or through copulation (Wickham et al. 1984).

[1]D. E. Wickham, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, pers. commun. November 1985.

TABLE 1.—Prevalence of the egg predator *Carcinonemertes errans* on Dungeness crabs collected in the Columbia River estuary from November 1983 through October 1985.

	Number examined	Number infested	Percent infested
Prevalence by month			
Nov. 1983	362	25	7
Dec. 1983	345	8	2
Jan. 1984	273	3	1
Feb. 1984	160	1	1
Mar. 1984	130	1	1
Apr. 1984	105	9	9
May 1984	84	8	10
June 1984	141	15	11
July 1984	146	6	4
Aug. 1984	248	18	7
Sept. 1984	306	9	3
Oct. 1984	169	11	7
Nov. 1984	218	5	2
Dec. 1984	158	4	3
Jan. 1985	264	1	0
Feb. 1985	59	0	0
Mar. 1985	311	3	1
Apr. 1985	135	6	4
May 1985	238	6	3
June 1985	287	5	2
July 1985	301	8	3
Aug. 1985	262	12	5
Sept. 1985	328	36	11
Oct. 1985	424	122	29
Total	5,454	322	mean, 6
Prevalence by size class			
Size class I	1,273	4	0
Size class II	2,561	102	4
Size class III	1,225	101	8
Size class IV	395	115	29
Prevalence by sex			
Male	3,269	155	5
Female	2,185	167	8

TABLE 2.—Prevalence of the egg predator *Carcinonemertes errans* on Dungeness crabs collected in nearshore areas of the Pacific Ocean from December 1983 through September 1985.

	Number examined	Number infested	Percent infested
Prevalence by month			
Dec. 1983	15	14	93
Jan. 1984	139	113	81
Mar. 1984	13	11	85
Apr. 1984	6	5	83
May 1984	4	3	75
June 1984	7	6	86
July 1984	10	6	60
Aug. 1984	20	17	85
Dec. 1984	5	2	40
Feb. 1985	3	0	0
Apr. 1985	16	15	94
May 1985	3	2	67
July 1985	37	29	78
Aug. 1985	11	7	64
Sept. 1985	130	99	76
Total	419	329	mean, 79
Prevalence by size class			
Size class I	46	1	2
Size class II	115	107	93
Size class III	151	124	82
Size class IV	107	97	91
Prevalence by sex			
Male	276	220	80
Female	143	109	76

Our data indicate that *C. errans* is a marine species that apparently cannot tolerate the lower salinities in the Columbia River estuary. It would be informative to examine Dungeness crabs from other Oregon and Washington estuaries with typically higher salinities to determine if infestation levels are comparable to those in the Columbia River estuary.

Acknowledgments

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SPRING AND SUMMER MOVEMENTS OF SUBADULT STRIPED BASS, *MORONE SAXATILIS*, IN THE CONNECTICUT RIVER[1]

The Connecticut River has no known spawning population of striped bass, *Morone saxatilis*, but there is an annual run of subadults in the late spring and summer from Long Island Sound to Holyoke Dam, 140 km upstream (Moffitt et al. 1982). In 1980-82, 80-90% were age II (the remainder were age III); about 60% were males (Warner 1983). The biological reason for such a run is unknown, but feeding may be an important attractant to the river. The major foods of striped bass collected at Holyoke Dam are spottail shiners, *Notropis hudsonius*, and the scales and body parts of adult American shad, *Alosa sapidissima*, and blueback herring, *A. aestivalis*, that result from injury or death at the hydropower dam and fish lifts or from angling (Warner and Kynard 1986). Factors other than food are undoubtedly important influences on the riverine migration.

The migration of subadult striped bass into natal or nonnatal rivers was documented by Raney et al. (1954) and Nicholas and Miller (1967), but the reasons for the movement are not clear. We hypothesized that detailed studies of subadult movements in the Connecticut River could help reveal some of the environmental factors that effect the movements. We used radio telemetry of subadults captured at Holyoke Dam to observe the use of river habitats, diel activity, and the rates of upstream and downward movements. We also investigated the passage of striped bass at the Holyoke fish lifts in relation to river temperature during 1979-86.

Study Area

Radio-tagged striped bass were observed after they were transferred above Holyoke Dam into the 53 km of the Connecticut River, between the Holyoke Dam and the Cabot Station hydroelectric facility which is below Turners Falls Dam (Fig. 1). The upstream 23 km reach is relatively straight, with few areas deeper than 4 m; the lower 30 km reach meanders, creating a deep channel and shoals (Fig. 1). Bottom type is rubble and gravel in the

[1]Contribution No. 94 of the Massachusetts Cooperative Fishery Research Unit, which is supported by the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries and the University of Massachusetts.

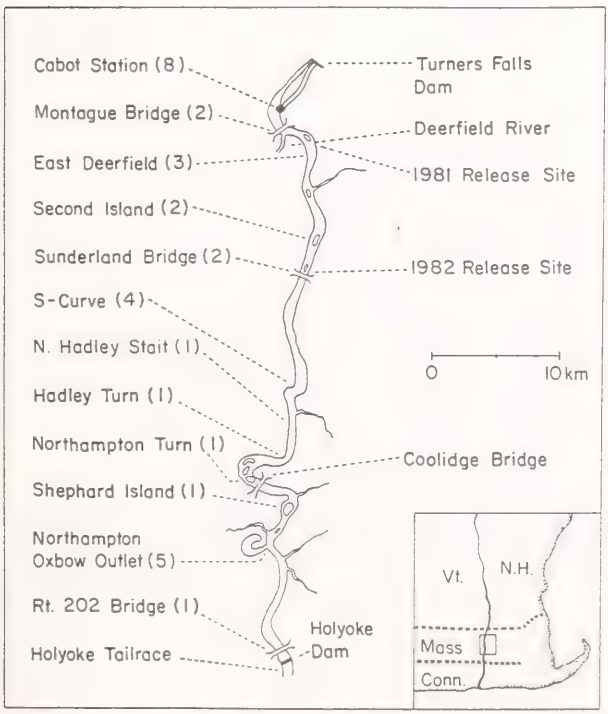

FIGURE 1.—The 53 km of the Connecticut River above the Holyoke Dam where the movements of radio-tagged striped bass were observed in 1981-82. The 13 holding areas where striped bass stopped are on the left side of the river (number of stops in parenthesis).

upper stretch; and sand and areas of exposed rock ledge are in the lower section (Armour 1966).

Methods

The number of striped bass passed daily by the Holyoke fish lifts from 1979 to 1986 was counted by personnel of the Massachusetts Cooperative Fishery Research Unit (MCFRU). Maximum daily river temperature recorded at the dam was used to characterize the temperature regime for the striped bass lifted each day. The daily records of each year's run were used to make frequency distributions of the number of fish lifted and the daily maximum temperature. We used the statistics of mean, median, standard deviation, and range of temperatures to visually compare the temperatures when striped bass entered the lifts.

All striped bass used for telemetry were captured during 1981 and 1982 in the fish trap at the lifts. To help reduce mortality caused by handling, we marked only the largest fish captured (280-365 mm fork length). Fish were held at the dam for a maximum of 5 d in a 1,325 L circular tank supplied with river water. At the release sites (Fig. 1), we inserted into the fish a transmitter which went directly through the mouth and into the stomach, a procedure that did not interfere with subsequent feeding (Warner 1983).

Radio transmitters were constructed using the design of Knight (1975) or with the modifications of Buckley (MCFRU). The transmitters measured 12 mm in diameter and 45 mm long, weighed 3.5-5.5 g in air, and transmitted for 7-21 d. Weight of the transmitters never exceeded 3.4% of the body weight of the fish. Individual fish were identified by 12 frequencies (30.05-30.25 MHz) and by variations in the pulse rate of each frequency.

We tracked striped bass from a boat using an omnidirectional antenna (1/8-wave, base loaded) to locate fish to within about 100 m and a directional, tuned-loop antenna to locate fish to within about 10 m. Locations of fish were noted on contour maps of the river. Initially, we tracked striped bass from 4 to 30 h, but tracking each fish was not continuous and depended on the speed of dispersal. Later, we surveyed the study area daily. Some striped bass moved actively and others were sedentary; therefore, we tracked the active fish continually for as long as 6 h, but only periodically noting the locations of others. In addition to the daily surveys, we observed some fish continually for 24 h to determine the diel movement; we conducted three diel surveys in 1981 and nine in 1982.

The upstream and downstream rates of movement (ground speed) were determined by using the continuous observations of striped bass that had been free longer than 1 h. Locations where striped bass remained longer than 90 min were designated as "holding areas". The physical characteristics of these areas were determined from visual observations and contour maps.

Results and Discussion

Passage in the Lifts and Temperature

Activity at the fish lifts appeared to be related to temperature (Fig. 2). Striped bass first entered the lifts when river temperatures were 17°-19°C (late May or early June), and in some years a few were still entering the lifts at 25°-28°C when lift operation ceased. The mean temperature of activity when striped bass entered the lifts ranged from a low in 1980 of 10.0°C to a high in 1983 of 23.4°C (Fig. 2). For the 7-yr period, the mean temperature of peak movement was 21.3°C (SD, 1.7°C) with 72% of the fish passage from 20°C to 24°C (85% of passage between 19° and 24°C).

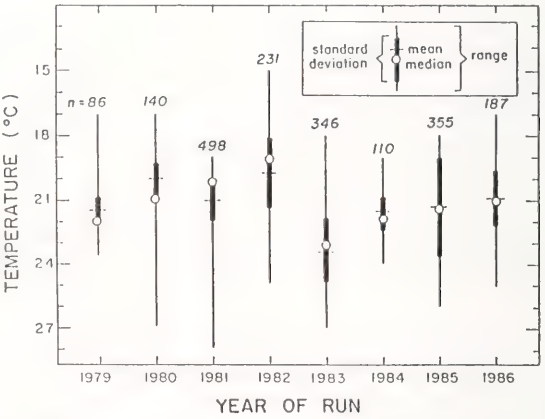

FIGURE 2.—Mean, median, standard deviation, and range of temperatures when subadult striped bass were passed in the Holyoke Dam fish lifts, 1979-86.

A recent hypothesis proposed that, as striped bass advance in age, they prefer cooler water (Coutant 1985). Further, the thermal niche of subadults (43-68 cm total length) in Tennessee reservoirs was 20°-24°C, when these temperatures were available (Coutant and Carroll 1980). This is essentially the same range as most upstream movement into lifts in this study. Although the movement of striped bass into

the lifts is more an indication of general activity than choice of preferred temperatures; nevertheless, the similarity in range of temperatures found in the two studies is remarkable. Striped bass began entering the fish lifts in late May when river temperatures were about 17°C. During mid- to late May 1979-83, the daily maximum temperatures in Long Island Sound near the mouth of the river were much cooler (12°-13°C, Millstone Laboratory, Northeast Utilities Service Co., Hartford, CT). While we do not know whether the striped bass overwinter in the lower river or enter fresh from Long Island Sound each spring, the movement of subadults from the cooler waters of the Sound into the warmer river is consistent with the thermal niche hypothesis of Coutant (1985). The only data from the Connecticut River that appears inconsistent with the hypothesis of Coutant (1985) is the capture of nine subadults in the lifts at Holyoke Dam in the fall of 1979 when river temperatures were 7°-10°C. Although prey abundance is high each fall at Holyoke Dam because of the outmigration and death of many juvenile American shad and blueback herring passed through the turbines (Taylor and Kynard 1985), the temperatures when the striped bass entered the lifts were much colder than preferred. Did the food abundance cause some striped bass to remain in water temperature that would otherwise be avoided? Because no striped bass have been lifted in the fall since 1979, we concluded that the event must be rare, whatever the reasons.

Radio Telemetry

We tagged 63 striped bass with transmitters: 11 in 1981 and 52 in 1982. Three tags failed immediately after release (all in 1982); therefore, 60 fish total were tracked. The study area was surveyed from late June to late July during 13 d in 1981 and 47 d in 1982.

Individual striped bass were tracked for periods of 1-14 d: 35 were tracked for ⩾1 d; and 25 were tracked for >2 d. Fish were tracked for an average of 4.3 d in 1981 (range: 1-14 d, N = 11) and 2.2 d in 1982 (range: 1-12 d, N = 46). Tracks of fish ended because of tag regurgitation, tag failure, and movement out of the study area. Operating tags were regurgitated by 15 fish (4 in 1981, 11 in 1982) averaging 3.6 d before regurgitation. There were four known tag failures after an average of 3.5 d of observations. Tracking the remaining 41 fish ended after they moved out of the study area or after undetected tag failure. No striped bass were observed moving upstream of the Cabon Station or into tributaries of the river. Surveys below Holyoke Dam located seven tagged fish, one 75 km downstream of Holyoke Dam near Hartford, CT. None of these fish returned to Holyoke Dam and they may have continued moving downstream to the Long Island Sound. Twenty additional fish were last observed moving downstream toward Holyoke Dam, and we expected that they also continued past the dam and, possibly, to the Sound. Because there was no spillage over the dam when many tagged fish returned downstream to Holyoke Dam, they passed the dam by entering one or more hydroelectric turbines.

Only striped bass tagged in 1982 moved upstream; the average upstream rate was 0.7 km/h (range: 0.30-1.2 km/h, N = 11). The mean rate of downstream movement was 1.9 km/h in 1981 (range: 1.0-3.2 km/h, N = 9); and 2.3 km/h in 1982 (range: 1.0-3.8 km/h, N = 21). Mean rates during the 2 years did not differ significantly (Student's t-test:$P >$ 0.05). One striped bass, which was located nine times during July 1982, traveled at least 143 km in the study area during 14 d.

Nine fish moving downstream in 1981 followed the channel of the river; 61 of 68 locations were in the channel at depths of 3-17 m. Although the actual proportion of deep-channel habitat compared with shoal habitat is unknown, there is much less channel than shoal area. Therefore, the preference for the channel appears strong, as was also found in telemetry studies of adult striped bass in Watts Bar Reservoir, TN (Cheek et al. 1985).

A total of 29 striped bass localized for periods of 90 min to 6 d in 13 different holding areas (Fig. 1). (Two localized at more than one area; therefore, a total of 33 such events were recorded.) Two fish were rarely found simultaneously at the same site. All holding areas, except the Route 202 Bridge site, were located near a bank of the river. The Cabot Station site accounted for 8 of the 33 localized periods and for most of the longest periods, i.e., two fish stayed at Cabot Station for 6 d each, one for 3 d, and three for 2 d.

Fish activity in holding areas was highly variable. Fish at Cabot Station moved in a stop-and-go manner during the day and night, in shallow and in deep water, and in the fast water of the power station discharge and in the slackwater upstream of the station. They appeared to be feeding in the discharge of the hydroelectric station—we have observed striped bass feeding in the discharge water of the Hadley Falls Hydroelectric Station at Holyoke Dam. Five fish were tracked at the outlet of the Northampton Oxbow (Fig. 1). All stayed in the main stem within 0.5 km of the outlet, moved in a stop-and-go

manner, and used three habitats: a low-flow turbid area, a 10 m deep channel, and sandy shoals upstream from the outlet. Movements at the S-curve (Fig. 1) and at other holding areas were highly variable: some remained in a small discreet area, others were inactive for long periods, and the rest moved actively within a 0.5 km reach of the river—similar to the movements at Cabot Station and at the Northampton Oxbow.

Striped bass followed several patterns of diel behavior. At Cabot Station, which has outside illumination at night, four moved actively during both the day and night. Koo and Wilson (1972) also found that adult striped bass were active at night in illuminated areas. At sites with natural illumination, the movements of 10 striped bass were as follows: 9 moved actively during the day; 6 stopped and 3 were less active at night; and 1 moved only at night. Of the 14 striped bass that we observed for 24 h, 10 increased their activity at dawn, dusk, or both. Dudley and McGahee (1983) found that adults were most active in late afternoon or evening, but noted an increased activity at dawn. Because striped bass feed most actively at dawn and dusk (Raney 1952), the increase in activity during these periods was probably related to feeding.

Based on the results of fish passage at Holyoke Dam, behavioral observations using telemetry, and the general thermal niche of subadults reported by Coutant and Carroll (1980) and Coutant (1985), we hypothesize that the movement of subadult striped bass into the Connecticut River is due in part to thermal preferences. The upriver migration in May-July places subadults in temperatures closer to their preferred range than those found in Long Island Sound. Tracking of fish in the river indicates a diverse behavioral range of active swimming, resting, and feeding that is consistent with a spring-summer period of high activity and growth. Local attraction to dam tailwaters provides access to abundant food (Warner and Kynard 1986), a feature that reinforces the advantages of following thermal cues into the riverine environment. The feeding advantages for striped bass will likely increase as the restoration program for American shad and blueback herring results in an increased abundance of juveniles.

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HABITAT PARTITIONING BY SIZE IN WITCH FLOUNDER, *GLYPTOCEPHALUS CYNOGLOSSUS*: A REEVALUATION WITH ADDITIONAL DATA AND ADJUSTMENTS FOR GEAR SELECTIVITY

In 1970, Powles and Kohler hypothesized separation of habitats of adult and juvenile witch flounder, *Glyptocephalus cynoglossus*, by depth based on surveys of Nova Scotia Banks and in the Gulf of St. Lawrence. Juveniles were sampled with a small mesh Icelandic shrimp trawl on the Nova Scotia Banks. These data were supplemented by data obtained from Squires' (1961) field records collected during shrimp surveys in the Cabot Strait and Gulf of St. Lawrence in the summers of 1957 and 1958 using a Norwegian deep-sea shrimp trawl. The authors concluded that during the summer months newly metamorphosed and small (<30 cm) witch flounder were found in the 180-288 m depth range.

Adult witch flounder (≥30 cm) were sampled with a No. 36 Yankee otter trawl on the Nova Scotia Banks from May to October and from November to April. Powles and Kohler (1970) concluded that adult witch flounder were most abundant at a depth range of 92-162 m. In winter months both adults and juveniles were found together in deeper water while in the summer both groups were separated.

Powles and Kohler (1970) suggested that this deepwater distribution of juvenile witch flounder could prevent direct competition with young of more abundant species such as Atlantic cod, *Gadus morhua*, and American plaice, *Hippoglossoides platessoides*, and provide a natural conservation against fishery exploitation. Their otter trawl catches, over a depth range of 36-450 m, yielded few juvenile witch flounder, although many small American plaice were captured. Escapement of juvenile witch flounder through the mesh in the wings of the trawl was ruled out because many small plaice were captured on the same grounds. The authors concluded that juvenile witch flounder were absent unless American plaice and witch flounder differed radically in behavior. Other studies of witch flounder depth distribution on the continental slope off Virginia (Markle 1975) and in the Gulf of St. Lawrence, NAFO (Northwest Atlantic Fisheries Organization) Divisions 4R and 4S (LaFleur and Lussiàa-Berdou 1982) supported the habitat separation hypothesis.

However, recent studies showed that a No. 36 Yankee shrimp trawl was more efficient in catching juveniles whereas a No. 41.5 Yankee otter trawl was more efficient in catching adult witch flounder (Walsh 1984). In that study juvenile American plaice and witch flounder co-occurred in the shrimp trawl catches; differential catches of witch flounder in the otter trawl was due to the escapement of juveniles. Apparent depth separation proposed by Powles and Kohler (1970) may have been based on data biased by gear selection.

Accurate descriptions of life history patterns of witch flounder are important for sound fisheries management, especially with regard to competition with other species and with regard to presumed mechanisms which protect from overfishing. Powles and Kohler (1970) derived their results from summer and winter surveys, and the conclusions were tentative because of potential gear selectivity problem. Therefore, I reevaluated the depth separation hypothesis with additional data taking gear selectivity into consideration.

Materials and Methods

Data used in the analysis were obtained from regular groundfish biomass surveys of the Gulf of St. Lawrence, NAFO Divisions 4R and 4S, by research vessels of the Northwest Atlantic Fisheries Centre, St. John's, Newfoundland, during the period 1978-80. In addition, two juvenile flatfish surveys were used: one in the northern Gulf of St. Lawrence, NAFO Division 4R, 1980; and one in the areas of Hermitage Bay and Fortune Bay, NAFO Division 3Ps, in 1981 (Fig. 1).

Fishing Gears and Research Designs

Groundfish surveys in September and October of 1978-80, NAFO Divisions 4R and 4S by the *A. T. Cameron* (side trawler) were conducted with a standard No. 41.5 Yankee otter trawl with a stretched mesh size of 127 mm in the wings and reducing to 111 mm in the cod end and a 30 mm mesh cod end liner was used. A total of 188-30 min fishing sets

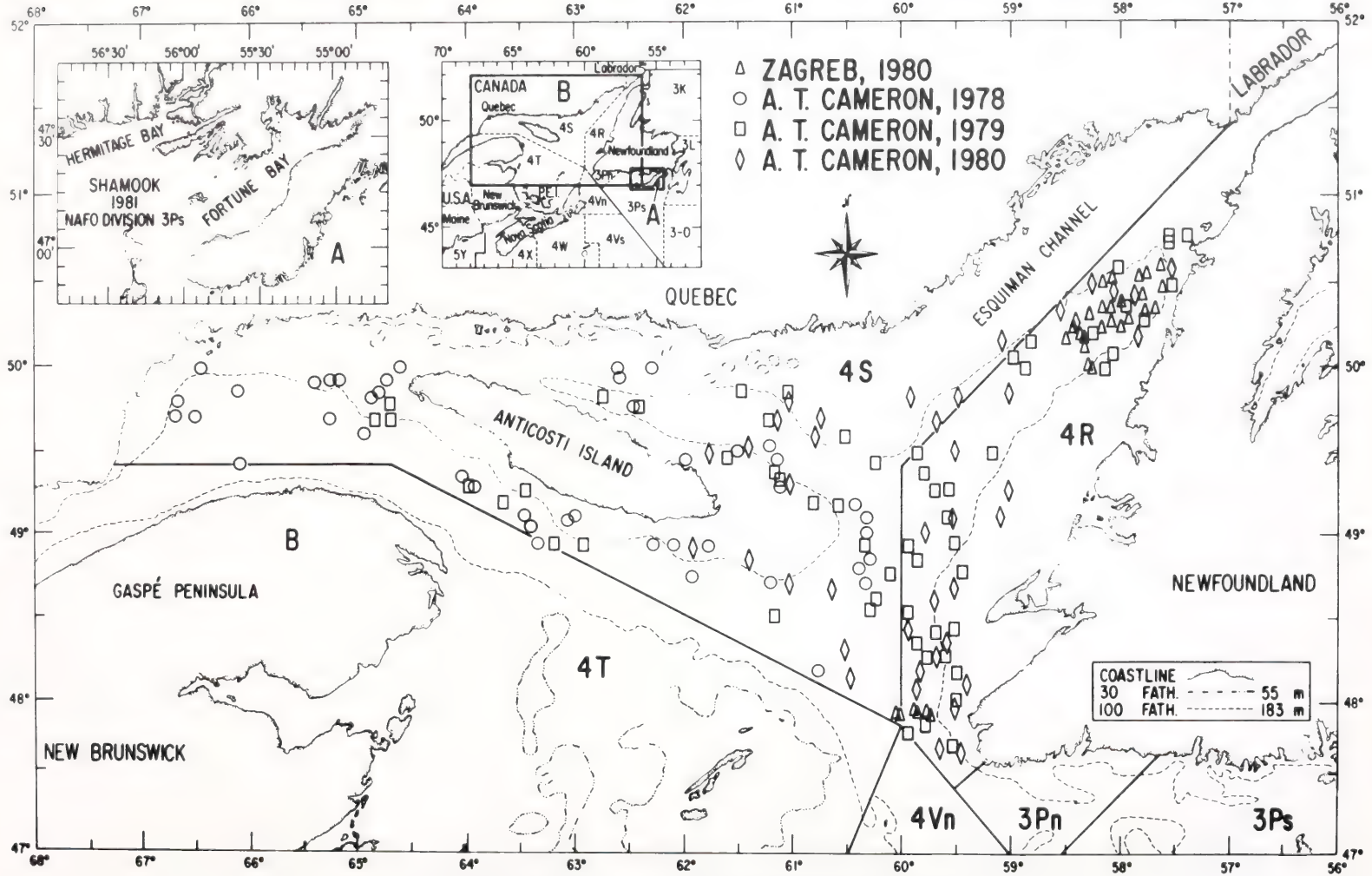

FIGURE 1.—Research vessel surveys of NAFO Division 4R, 4S, and 3Ps.

were made using a random stratification scheme (Fig. 1).

Both juvenile flatfish surveys used a No. 36 Yankee shrimp trawl, with a 38.1 mm mesh throughout and a 12.7 mm cod end mesh liner. The September 1980 survey was in the northern Gulf of St. Lawrence, NAFO Division 4R aboard the chartered stern trawler *Zagreb*. The trawl was equipped with a single tickler chain for approximately 53% of the fishing sets (see Walsh 1984). A total of 53 30-min fishing sets were made (Fig. 1). The October 1981 juvenile survey was in Hermitage Bay and Fortune Bay aboard RV *R. V. Shamook*. A total of 28 fishing sets in depths of 188-402 m were used in the analysis. Most of these sets were of <30-min duration owing to otter doors being stuck in the heavy mud of these bays and the catches were adjusted upward based on the ratio of actual tow to the standard 30 min (Fig. 1A). Both juvenile surveys were based on line transects that ran perpendicular to depth contours so that all depth zones would be sampled. Stations in the Gulf of St. Lawrence were about 10 mi apart on each line while the surveys in the two bays were about 2 mi apart. The purpose of these two surveys was to test the use of a small mesh trawl and delineate depth distribution of all flatfishes in the area sampled.

Method of Analysis

Total lengths of witch flounder were grouped into 2 cm intervals for the analysis. Catches of witch flounder at each station were divided into two size categories: juveniles (<30 cm) and adults (≥30 cm). Majority of witch flounder are sexually immature at 30 cm (Powles and Kohler 1970; Beacham 1983). Depths of catches were broken down at 20 m intervals and a Kolmogorov-Smirnov two-sample test was applied (Siegel 1956) to the cumulative distribution of both size categories for each data set. The null hypothesis used states that there is no difference in depth distribution of juvenile and adult witch flounder; i.e., the values of the population from which the juvenile sample and the adult sample were drawn have the same cumulative distribution. The alternative hypothesis used stated that there was a difference in depth distribution, i.e., the two-sample cumulative distributions were far apart and suggests the samples came from different populations. The level of significance used was $\alpha = 0.05$. A catch frequency was calculated for each size group over 20 m depth intervals.

The analysis was used on five data sets: 1) otter trawl catches for 1978-80 in both Division 4R and Division 4S were combined to increase sample size and coverage of the Gulf of St. Lawrence; 2) otter trawl catches in Division 4R, 1980 were used to compare with 3) shrimp trawl catches in Division 4R, 1980; 4) shrimp trawl catches in Division 3Ps; and 5) combination of the catches of both gears from sets north of lat. 50°N in Division 4R, 1980. The latter combination of data was used for two reasons: 1) There were no successful sets made by the shrimp trawl in depths <180 m owing to rough bottom while the otter trawl had sets in depths as shallow as 120 m, both vessels were in the same area at the same time, and 2) given a bias in gear selectivity, combination of catches of both gears should be representative of the population located in this small area of northern Esquiman Channel (Fig. 1).

Results

Trends in depth distribution of witch flounder using different fishing gears showed no significant difference in the cumulative distributions of juvenile and adult witch flounder in all data sets ($P > 0.05$) (Table 4).

No. 41.5 Yankee Otter Trawl

Divisions 4R and 4S, 1978-80. Juveniles were found in a depth range of 102-464 m with a median located in the 241-260 m depth interval. Adults were distributed in a depth range of 91-484 m with the median located in the 181-200 m depth interval (Table 1, Fig. 2A).

Division 4R, 1980. Both juveniles and adults were distributed in a depth range of 122-464 m. Most of the juveniles were located in the 241-260 m depth interval while the median of the adult witch flounder was located in the 160-180 m depth interval (Table 1, Fig. 2B).

No. 36 Yankee Shrimp Trawl

Division 4R, 1980. Juvenile and adult witch flounder were widely distributed in a depth range of 187-502 m. The median of juveniles was located in the depth interval 241-260 m while for adults it was the 261-280 m interval (Table 2, Fig. 2C).

Division 3Ps, 1981. Juvenile and adult witch flounder were widely distributed in a depth range of 188-402 m. The median of juvenile distribution was in the 281-300 m interval while that for adults was in the 261-280 m interval (Table 2, Fig. 2D).

TABLE 1.—Cumulative frequency of juvenile (<30 cm) and adult (≥30 cm) witch flounder catches over 20 m depth intervals using a No. 41.5 Yankee otter trawl.

Depth 20 m intervals	NAFO Div. 4R and 4S, 1978-80						NAFO Div. 4R, 1980					
	Nos. <30 cm	%	Cumulative %	Nos. ≥30 cm	%	Cumulative %	Nos. <30 cm	%	Cumulative %	Nos. ≥30 cm	%	Cumulative %
81-100	0	0	0	6	0.34	0.45						
101-120	2	0.11	0.47	4	0.22	0.74						
121-140	0	0	0.47	20	1.12	2.23	0	0	0	2	1.08	1.32
141-160	11	0.62	3.02	142	7.99	12.76	2	1.08	5.88	61	32.97	41.72
161-180	36	2.02	11.40	415	23.34	43.55	6	3.24	23.53	42	22.70	69.54
181-200	13	0.73	14.42	148	8.32	54.53						
201-220	15	0.84	17.91	82	4.61	60.61	1	0.54	26.47	7	3.78	74.17
221-240	90	5.06	38.84	59	3.32	64.99						
241-260	90	5.06	59.77	35	1.97	67.58	5	2.70	41.18	8	4.32	79.47
261-280	41	2.31	69.30	55	3.09	71.66						
281-300	38	2.14	78.14	110	6.19	79.82	3	1.62	50.00	5	2.70	82.78
301-320	9	0.51	80.23	33	1.86	82.27	5	2.70	64.71	6	3.24	86.75
321-340	9	0.51	82.33	64	3.60	87.02	1	0.54	67.65	4	2.16	89.40
341-360	5	0.28	83.49	15	0.84	88.13	2	1.08	70.58	1	0.54	90.07
361-380	31	1.74	90.70	59	3.32	92.51						
381-400	11	0.62	93.26	32	1.80	94.88						
401-420	8	0.45	95.12	7	0.39	95.40	8	4.32	97.06	7	3.78	94.70
421-440	3	0.17	95.81	6	0.34	95.85						
441-460	15	0.84	99.30	45	2.53	99.18						
461-480	3	0.17	100.00	10	0.56	99.93	1	0.54	100.00	8	4.32	100.00
481-500	0	0	—	1	0.06	100.00						
Total	430			1,348			34			151		

TABLE 2.—Cumulative frequency of juvenile (<30 cm) and adult (≥30 cm) witch flounder catches over 20 m depth intervals using a No. 36 Yankee shrimp trawl.

Depth 20 m intervals	NAFO Div. 4R, 1980						NAFO Div. 3Ps, 1981					
	Nos. <30 cm	%	Cumulative %	Nos. ≥30 cm	%	Cumulative %	Nos. <30 cm	%	Cumulative %	Nos. ≥30 cm	%	Cumulative %
180-190	210	4.69	4.91	43	0.96	21.18	10	0.91	2.70	42	3.83	5.87
191-200	—	—	—	—	—	—	—	—	—	—	—	—
201-220	135	3.01	8.07	5	0.11	23.65	9	0.82	5.12	51	4.69	12.79
221-240	640	14.29	23.04	15	0.33	31.03	31	2.82	13.48	103	9.38	26.96
241-260	1,194	26.26	50.97	18	0.40	39.90	8	0.73	15.63	112	10.20	42.37
261-280	1,209	27.00	79.25	36	0.80	57.64	28	2.55	23.18	74	6.74	52.54
281-300	372	8.31	87.95	21	0.47	67.98	110	10.02	52.83	118	10.75	68.78
301-320	98	2.19	90.25	4	0.09	69.95	15	1.37	56.87	6	0.55	69.60
321-340	242	5.40	95.91	8	0.18	73.89	15	1.37	60.92	29	2.64	73.59
341-360	29	0.65	96.58	1	0.02	74.38	105	9.56	89.22	174	15.85	97.52
361-380												
381-400												
401-420	—	—	—	—	—	—	40	3.64	100.00	18	1.69	100.00
411-440												
441-460												
461-480	76	1.70	98.36	39	0.87	93.60						
481-500	19	0.42	98.81	2	0.04	94.58						
501-520	51	1.14	100.00	11	0.25	100.00						
Total	4,275			203			371			727		

No. 36 Yankee Shrimp Trawl Combined with No. 41.5 Yankee Otter Trawl

Division 4R, North of Lat. 50°N, 1980. The median of juvenile distribution was located in the 240-260 m interval while that for adults was located in the 180-200 m depth interval (Table 3, Fig. 3).

Discussion

The results of the analysis do not statistically support the hypothesis that juvenile witch flounder prefer a deeper water habitat than adults, although the median usually shows adults shallower than juveniles. Only the shrimp trawl catches in NAFO Division 4R, 1980 show juveniles shallower than adult witch flounder (Fig. 2C). Combining the data

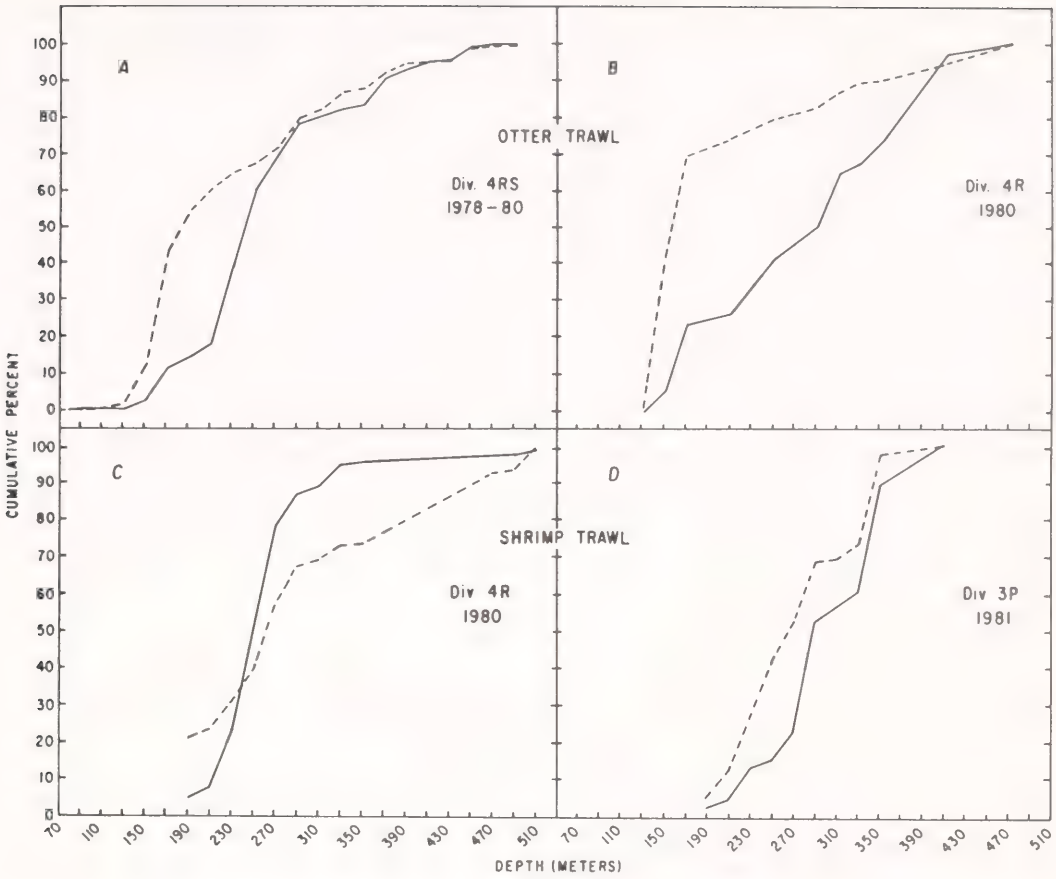

FIGURE 2.—Cumulative frequency distribution of juvenile and adult witch flounder by both fishing gears. Dash line: adults (≥30 cm); solid line: juveniles (<30 cm). A) No. 41.5 Yankee otter trawl, Division 4RS 1978-80 combined. B) No. 41.5 Yankee otter trawl, Division 4R 1980. C) No. 36 Yankee shrimp trawl, Division 4R, 1980. D) No. 36 Yankee shrimp trawl, Division 3Ps, 1981.

sets from two fishing gears for analysis of the northern Esquiman Channel area of NAFO Division 4R in 1980 takes into account biases in gear selectivity (Fig. 3). In this study of the Gulf of St. Lawrence, juveniles are more vulnerable to shrimp trawls as Powles and Kohler (1970) showed in their study. Low catches of adult witch flounder in all data sets indicate that they are widely dispersed and not readily accessible in any large numbers regardless of fishing gears used. A discrete separation of adults and juveniles does not exist. Although a large percentage of adult witch flounder are found

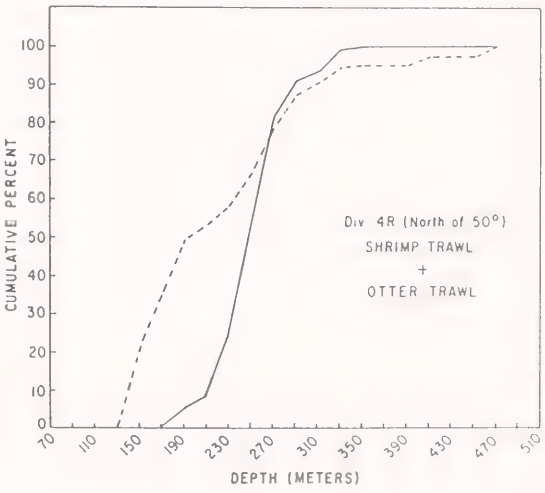

FIGURE 3.—Cumulative frequency distribution of juvenile and adult witch flounder in the Northern Esquiman Channel area (north of lat. 50°N). Catches of a No. 41.5 Yankee otter trawl and No. 36 Yankee shrimp trawl combined. Division 4R, 1980.

TABLE 3.—Cumulative frequency of juvenile (<30 cm) and adult (≥30 cm) witch flounder catches over 20 m depth intervals. Catches of a No. 41.5 Yankee otter trawl (8 sets) and a No. 36 Yankee Shrimp trawl (48 sets) combined for the northern Esquiman Channel area (lat. 50°N).

Depth 20 m intervals	NAFO Div. 4R, 1980: Sets north of 50°N					
	Nos. <30 cm	%	Cumulative %	Nos. ≥30 cm	%	Cumulative %
120-140	0	0	0	2	0.04	0.66
141-160	2	0.09	0.05	61	1.37	20.86
161-180	6	0.13	0.19	42	0.94	34.77
181-200	2.0	4.70	5.24	43	0.96	49.01
201-220	136	3.05	8.50	12	0.27	53.98
221-240	640	14.33	23.88	15	0.34	57.95
241-260	1,199	26.85	52.68	26	0.58	66.56
261-280	1,209	27.08	81.72	36	0.81	78.48
281-300	375	8.40	90.73	26	0.58	87.09
301-320	103	2.31	93.20	10	0.22	90.40
321-340	243	5.44	99.04	12	0.27	94.37
341-360	31	0.69	99.78	2	0.04	95.03
361-380	—	—	99.78	—	—	95.03
381-400	—	—	99.78	—	—	95.03
401-420	8	0.18	99.98	7	0.16	97.35
421-440	—	—	99.98	—	—	97.35
441-460	—	—	99.98	—	—	97.35
461-480	1	0.02	100.00	8	0.18	100.00
Total	4,163			302		

TABLE 4.—Results of Kolmorgov-Smirnoff two sample test on each data set. Level of significance used was $\alpha = 0.05$.

Fishing gear	Year	NAFO Divisions	Total no. juveniles	Total no. adults	D statistic	Table value	Significant at $\alpha = 0.05$
No. 41.5 Yankee otter trawl	1978-80	4RS	430	1,348	0.4270	0.0753	Not significant
No. 41.5 Yankee otter trawl	1980	4R	34	185	0.4770	0.2582	Not significant
No. 36 Yankee shrimp trawl	1980	4R	4,275	203	0.2220	0.0977	Not significant
No. 36 Yankee shrimp trawl	1981	3Ps	371	727	0.2936	0.0868	Not significant
No. 41.5 Yankee otter trawl + No. 36 Yankee shrimp trawl	1980 Sets north of lat. 50°N.	4R	4,163	302	0.4448	0.0810	Not significant

shallower than juveniles in the 100-200 m range, they are also found in sufficient numbers in all depths >200 m (Table 1). LaFleur and Lussiàa-Berdou (1982) research surveys in the Gulf of St. Lawrence using a Yankee 41.5 otter trawl found juveniles in the 200-300 m depth range and, while supporting Powles and Kohler's (1970) depth separation hypothesis also noted that even at depths >300 m, a significant proportion of adult witch flounder were caught. W. R. Bowering (Department of Fisheries and Oceans, St. John's, Newfoundland, pers. commun. 1986) has found that adult witch flounder in NAFO Division 2J3KL also exhibit two peak concentrations: one at 101-200 m and a second one in depths >300 m. That adult witch flounder are not concentrated during summer months is the reason why an economical commercial fishery only occurs during winter months (Powles and Kohler 1970; Bowering and Pitt 1974; Bowering and Brodie 1984).

Catches of witch flounder in the 1981 shrimp trawl survey of the two deepwater bays in NAFO Division 3Ps shows that although adults are usually average shallower than juveniles, they are also dispersed across deeper depth zones (Table 1). This suggests that in confined areas of deepwater bays, distribution patterns of adult witch flounder is more concentrated than in large open areas like the Gulf

of St. Lawrence. Similarly, adult witch flounder have been reported concentrated in the deepwater of St. Georges Bay, NAFO Division 4R during the summer months where a localized fishery occurs in depths of 300 m (Bowering and Brodie 1984).

In conclusion, juvenile witch flounder are distributed differently than the adult population off continental shelf areas of the Gulf of St. Lawrence. However, the two populations are not discretely separated as proposed by Powles and Kohler's (1970) niche separation hypothesis. Bowers (1960) concluded that witch flounder in the Irish Sea have no definitive separation. Heavy exploitation of juvenile witch flounder is prevented by the behavior of this size group making them less vulnerable to commercial otter trawls. The difference may be related to difference in preferred food items or distribution of predators. Further research is required to establish the mechanisms for the difference in depth distribution documented by this study.

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MOVEMENT OF TAGGED LINGCOD, *OPHIODON ELONGATUS*, IN THE PACIFIC NORTHWEST

Lingcod, *Ophiodon elongatus*, is a commercially and recreationally important West Coast species. Most previous studies have indicated that lingcod is a relatively nonmigratory species (Hart 1943; Chatwin 1956; Phillips 1959). More than 90% of the adults remained within 5 mi (8.1 km) of the point of tagging for as long as several years.

We tagged lingcod in the eastern Strait of Juan de Fuca and near San Juan Island, WA, from 1976 and 1981. We present results from tags returned by fishermen through 1985. The tag returns were analyzed primarily to show the extent of migration. We also analyzed recaptures by sex, size, direction of movement, and the effects of tag type and the location of tagging.

Methods

From 1976 to 1978, relatively small numbers of lingcod were tagged, incidental to a tagging study directed to rockfish (*Sebastes* sp.) (Mathews and Barker 1984), in which rod-and-reel with artificial lures was used to capture fish for tagging. From 1979 to 1981 tagging effort was for lingcod using a chartered commercial vessel trolling with a string of 6-10 jigs or other artificial lures from a hydraulic gurdy.

A total of 1,692 lingcod were tagged during 1976-81. Most of the lingcod (over 90%) were tagged during March through May. When caught singly, they were immediately tagged and released. If several lingcod were brought aboard at the same time, they were held in a circulating seawater tank until tagged. All tagged fish were measured (fork length) to the nearest millimeter. From 1978 to 1981, sex was determined by the presence of the anal papillae in males. Only fish not injured by capture were tagged and released. Those that bled, or that were hooked in the gills or throat, or that otherwise appeared disabled were not tagged.

Three types of spaghetti end tags were used: Anchor with #20 tubing (Floy[1] FD-67, Floy Co., Seattle, WA); small dart with #20 tubing (Floy FT-2); and large dart with #13 tubing (Floy FT-1). The tagging area and number tagged at each location are shown in Figure 1. The principal tagging locations were Middle Bank, a low relief, hard rubble bottom bank of about 6 km^2 and 20-60 m deep; Hein Bank, of similar area to Middle Bank but shallower (6-30 m deep), having a softer bottom and extensive kelp beds; and San Juan Channel, a passage with high relief, rocky substrate 2-6 km wide, coursing among several of the San Juan Islands. Most of the tagging in San Juan Channel was done near Turn Island in about 30 m of water. A few lingcod were tagged at other locations near San Juan Island.

Recapture information, including primarily the date and place of capture, was obtained from tags

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

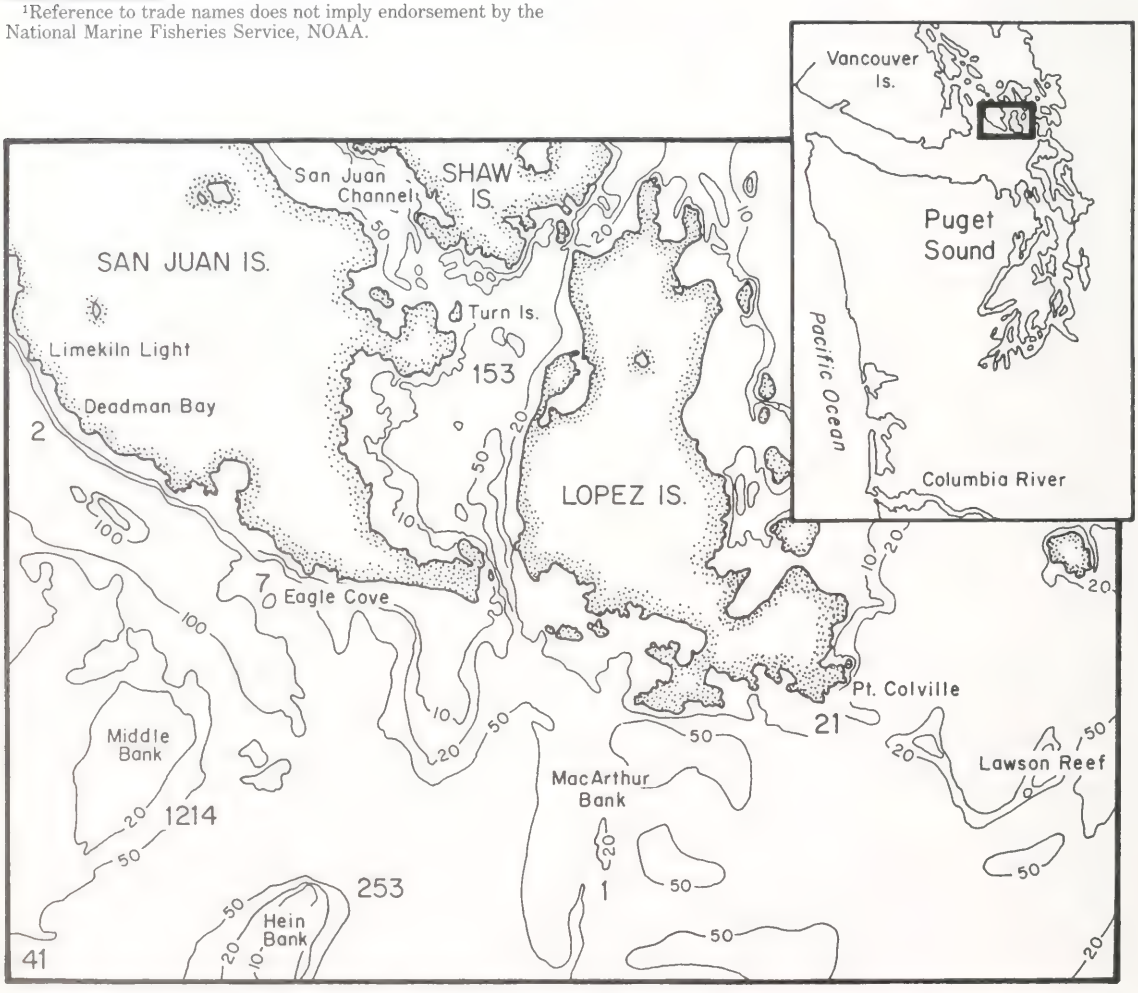

FIGURE 1.—Lingcod tagging area in relation to western Washington. Small numbers show depth contours in fathoms (1 fathom = 1.829 m) and large numbers show numbers tagged by location.

returned voluntarily by sport fishermen and commercial troll and trawl fishermen. A $2 reward was offered for the return of the tags. Several fishermen were personally contacted to clarify the information they provided and to seek specific information on where and how they fished; all the fishermen were cooperative. Assuming these fishermen were representative of all those who returned tags, we believe that the overall recovery information was accurate.

The size and sex distributions of the tagged lingcod are shown in Graphs I, II, and III of Figure 2. Eighty-six percent of all tagged lingcod were sexed, and of this sample 87% were males. The reported size ranges at maturity are 40-46 cm for males and 70-76 cm for females (Forrester 1969; Hart 1973).

Operationally, we define migratory and nonmigratory lingcod as fish recaptured at distances greater than and <8.1 km (5 mi), respectively, from the tagging site. This reference distance has been used for similar purposes in previous tagging studies. Since the recovery locations were usually given by the name of a geographical location such as "Middle Bank" or "Turn Island", there was some imprecision in estimating the distance moved. However, the fishing area associated with such named locations is <8.1 km in diameter. Thus, for example, a fish tagged on Middle Bank and recaptured on Middle Bank was assumed to have travelled <8.1 km.

Chi-square contingency table analysis was used for comparing recapture rates by tag type and sex, for comparing release-length frequency distributions of migratory and nonmigratory recoveries, and for comparing migrational tendencies by sex. A chi-square goodness of fit test was used to test the null hypothesis that the release-length distribution of all recaptured lingcod was the same as that of all tagged lingcod. For both of the length-frequency tests, lengths were grouped into 5 mm intervals, but at the tails of the distribution the intervals were wider than 5 mm to follow the rule for chi-square analysis that no expected cell frequency should be <1.0 and that no more than 20% of expected cell frequencies should be <5.0 (Zar 1974, p. 50). One-way analysis of variance was used to test the null hypothesis that the average time between tagging and recapture was the same for fish that had migrated different distances.

Most of our tagged males and about half of our tagged females were large enough to be reproductively mature when tagged.

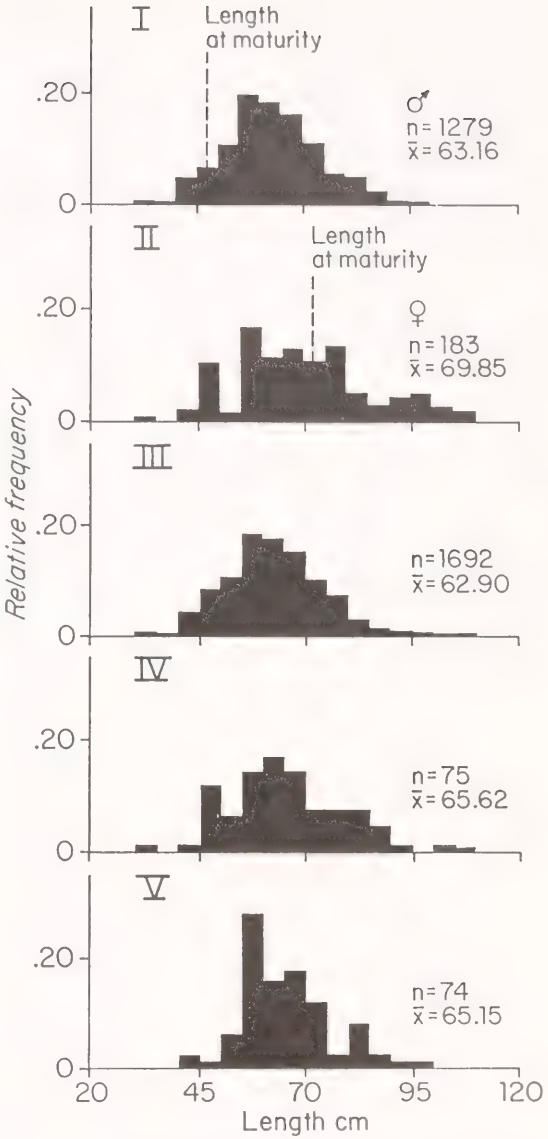

FIGURE 2.—Length-frequency distributions of tagged lingcod. I - known male lingcod tagged; II - known female lingcod tagged; III - all lingcod tagged; IV - release length distribution of all tagged lingcod recovered less than 8.1 km from release location; V - release length distribution of all tagged lingcod recovered more than 8.1 km from release location.

Results

There were no significant differences among recovery rates by tag type ($\chi^2 = 1.90$ with 2 df; $0.26 < P < 0.50$) (Table 1). However, we suspect from limited double-tagging and aquarium holding of tagged fish that the large dart had better retention qualities for lingcod than the other two tag types.

Through October 1985, 157 (9.3%) tagged lingcod

TABLE 1.—Rates of recapture of tagged lingcod for three types of tags.

Tag type	No. of lingcod tagged	No. of tags returned by fishermen	% returned
Anchor (Floy FD-67)	82	7	8.5
Small dart (Floy FT-2)	687	66	9.0
Large dart (Floy FT-1)	979	88	9.2
Total	[1]1,748	[2]161	

[1]Includes 56 fish which were double tagged with two different tag types.
[2]Includes four recoveries of double tagged fish with both tags remaining.

were recaptured. Recaptures were reported for up to 6 years following the year of tagging (Table 2).

Of the 149 lingcod with known tagging and recapture locations, 75 were recaptured <8.1 km from the tagging location and judged to be nonmigratory, whereas the remaining 74 were judged to be migratory, having been recaptured at distances >8.1 km from the tagging location (Table 3). Of the 74 that migrated, 61 were recaptured 8.1-50 km from the tagging location and 13 were recaptured farther than 50 km from the tagging location. The extent of migration depended on the location of the tagging site. Only one of 15 recaptured lingcod tagged in San Juan Channel migrated, whereas 70 of 117 (60%) tagged at Middle Bank and Hein Bank migrated (Table 3).

The predominant pattern of movement was west and south through the Strait of Juan de Fuca; 65 of the 74 migratory lingcod were recaptured south and west of the tagging site, but only 9 were recovered north and east of the tagging site (Table 3). The null hypothesis that lingcod were as likely to go south/west as north/east was rejected (χ^2 = 42.4 with 1 df; $P < 0.001$). Five recaptures from the Pacific Ocean were reported; the one farthest from the tagging location was caught off Newport, OR, a migration of 564 km.[2] The longest migration to the north/east was to Porlier Pass, BC, Canada, about 75 km from the tagging site. The greatest number of recaptures (34) was from Constance Bank, located in Canadian waters about 18 km west of Middle Bank. Most of the Constance Bank recaptures were made by Canadian trawlers. About one third of the total reported recaptures were taken in Canadian waters and two thirds in U.S. waters,

[2]This unusual recovery location was verified by follow-up correspondence. The fish was recaptured 6.5 yr after tagging by a small coastal trawler that usually fished 3-8 mi off Newport's south jetty.

TABLE 2.—Number of lingcod tagged, 1976-81, and recaptured through 1985 by year of recapture.

Year tagged	No. tagged	Number recaptured by year												% recaptured
		1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	Unknown[1]	Total	
1976	41	1	2	0	1	0	0	1	0	0	0	0	5	12.2
1977	101		1	5	4	1	0	0	2	0	0	0	13	12.9
1978	87			1	4	0	2	0	0	0	0	0	7	8.0
1979	507				8	24	5	4	1	0	1	0	43	8.5
1980	535					19	14	3	4	0	1	0	41	7.7
1981	421						29	7	7	1	1	1	46	10.9
Unknown[2]	—					1	1	0	0	0	0	0	2	—
Total	1,692	1	3	6	17	45	51	15	14	1	3	1	157	9.3

[1]Year of recapture not reported.
[2]Tag number unreadable when recaptured.

TABLE 3.—Distribution of recoveries of tagged lingcod by location of tagging, distance of migration and direction of migration.

Tagging location	No. tagged	No. recovered <8.1 km from tagging location	No. recovered farther than 8.1 km from tagging location				Recovery location unknown relative to tag location	Total recaptured	% recaptured
			8.1-50 km W and/or S	>50 km W and/or S	8.1-50 km E and/or N	>50 km E and/or N			
Middle Bank	1,214	47	50	6	4	4	6	117	9.6
Hein Bank	253	10	3	2	1	0	0	16	6.3
San Juan Channel	153	14	1	0	0	0	0	15	9.8
Miscellaneous	72	4	2	1	0	0	0	7	9.7
Unknown[1]	—	—	—	—	—	—	2	2	—
Total	1,692	75	56	9	5	4	8	157	9.3

[1]Tag number unreadable when recaptured.

which indicates that lingcod in the study region are an international resource.

The time between tagging and recapture averaged 18 mo (Table 4) and did not differ significantly by the distance traveled ($F_{2,128} = 1.32$; $0.25 < P < 0.50$).

The majority of the nonmigratory recaptures were caught in May-July, but the migratory fish were caught mostly in August-October. This difference could not be attributed to any seasonal pattern of migration and was probably a sampling artifact. Fishing effort by commercial trollers and sport fishermen in the tagging areas peaked during May-July, while the fishing effort of the trawl fleet on Constance Bank, from which many of the migratory recaptures came, peaked in late summer and fall (Smith 1981; Leaman 1982, 1983, 1984).

We found that migratory tendency apparently did not depend on individual size. Figure 2 shows a comparison of the release length-frequency distributions of lingcod recaptured <8.1 km (Graph IV) and more than 8.1 km (Graph V) from release location. The null hypothesis that migratory and nonmigratory lingcod have the same length distribution was accepted ($\chi^2 = 13.09$ with 10 df; $0.10 < P < 0.25$).

The release-length distribution of all recaptured lingcod was significantly different from that of all tagged lingcod ($\chi^2 = 25.42$ with 10 df; $P < 0.01$); release lengths of recaptured lingcod averaged slightly larger than those of all tagged lingcod (Fig. 2, Graphs III, IV, and V).

Recaptured lingcod offered no evidence that males and females differ in migratory behavior. Recapture rates were virtually the same for the two sexes. The null hypothesis that male and female tagged recoveries represent two populations with equal proportions of nonmigratory and migratory individuals was accepted ($\chi^2 = 3.14$ with 1 df; $0.05 < P < 0.10$) (Table 5). However, numbers of females tagged and recaptured were so low that any conclusion from this comparison should obviously be drawn with caution.

TABLE 4.—Time span between date of tagging and date of recapture for tagged lingcod recoveries with known month of recapture.

Recoveries by distance between tagging and recapture locations	No.	Time span (mo.) $\bar{X}$	Range
<8.1 km	75	15.1	0-71.2
8.1-50 km	55	18.6	3.2-76.0
>50 km	11	18.0	2.2-76.6
Total	131	18.0	0-76.6

TABLE 5.—Distributions by sex of the lingcod recaptured <8.1 km from the tagging location and of those recaptured >8.1 km from the tagging location.

Sex	No. tagged and sexed	Number recaptured <8.1 km	>8.1 km	Total	% recaptured
Male	1,279	57	63	120	9.4
Female	183	12	5	17	9.3

Discussion

The highly imbalanced sex ratio of the tagged fish can be explained by different depth distributions of the two sexes. Others have found, as we did on our tagging cruises, that female lingcod tend to reside deeper than males (Chatwin 1956; Miller and Geibel 1973; Cass et al. 1984). Most of our tagging effort was at depths of 25-30 m where the abundance of lingcod regardless of sex was the greatest. We fished in depths down to 100 m and found that relative abundance of females increased with depth.

The reason that the small tagged individuals tended to be recaptured at a lesser rate than the larger ones could be the higher natural mortality of small lingcod within the size range of our tagged sample. Lingcod are renowned for their cannibalism (Chatwin 1956; Phillips 1959), which could be a likely source of size-dependent mortality.

Our results show more lingcod migratory behavior than most previous studies. Hart (1943) reviewed recovery information from 1,993 lingcod tagged during 1939-43 throughout the Strait of Georgia, BC, Canada, and stated that "some but not more than 5% of lingcod are more or less migratory." Chatwin (1956) summarized Hart's data together with information from additional tagging in the Strait of Georgia through 1954 and found that of 342 total recaptures, 41 (12%) moved more than 1 mi (1.6 km) but <5 mi (8.1 km) from the point of tagging, and 32 (9.3%) moved farther than 5 mi. Chatwin therefore concluded that lingcod was a relatively sedentary species with no well-defined migration pattern. Phillips (1959) reviewed the above two papers and concluded from these and other tag recovery observations in the literature that lingcod is a nonmigratory species, particularly after reaching maturity.

Reeves (1966) reported on results from tagging 437 lingcod on 40-Mile Bank, which is about 50 km west of Cape Flattery, WA. The overall recapture rate was very high because of an intensive trawl fishery for lingcod in the vicinity of tagging; 53.3% of all tagged fish were recaptured within 6 wk of release. Only 5% of the recaptures were farther than 5 mi (8.1 km) from the tagging site. However, the

number of fish migrating may have been affected by the trawl fishery which could have removed potential migrants.

Cass et al. (1983b) reported results from tagging 2,997 lingcod off the west coast of Vancouver Island, BC, and 752 in the Strait of Georgia, BC, in 1978. However, the combined recovery rate through 1982 was so low (1%—apparently because of the excessive mortality from too high a dosage of oxytetracycline that was injected intraperitoneally in an attempt to validate aging methods) that little could be concluded on movements. Of the 21 recaptures with known recapture location, 4 (19%) had traveled more than 20 km. One of these was caught off central Oregon, 510 km from the tagging sites.

Further Canadian tagging efforts off southwest Vancouver Island in July 1982 and in the Strait of Georgia in 1982-83 are reported by Cass et al. (1983a) and Cass et al. (1984), respectively. Off Vancouver Island, 7,429 lingcod were tagged and 1,442 (19%) were recaptured through 1982. Very little movement was indicated, since 97% of the recaptures were taken in the area of release by Canadian trawlers. As with the Reeves' (1966) study, the initial recapture rates were very high because of intensive trawling in the tagging area. The Strait of Georgia tagging effort indicated relatively little movement. A total of 3,991 lingcod were released from November 1982 to March 1983 in three areas: Campbell River (76%), Pender Harbor (16%), and Stuart Island (8%). Through November 1983, 392 recaptures were reported by sport and commercial fishermen, and location of recovery was known for 383 of these. Of the latter number, 354 (92%) were recaptured within 5 km of their release site and 235 of these (61%) showed no detectable movement. From these observations the authors concluded that lingcod do not undertake extensive short-term movements.

We are aware of only one other lingcod tagging study that shows migration similar to that in the present study. H. Horton[3] reported results from 552 lingcod tagged on the central Oregon coast from June 1978 to January 1982. Nineteen recaptures were reported through 1985: 10 had not moved significantly and 9 had migrated more than 10 km. Of those that migrated, 2 went a distance of more than 100 km.

Our study gives evidence that certain populations of lingcod have a high proportion of individuals likely to migrate. Large, mature individuals may have migration patterns similar to individuals smaller than the reported sizes at maturity. The movement pattern in our tagged sample was directional, not random. In assuming that the fraction of total recaptures more than 8.1 km from the tagging site represents the migration within the population, we also assumed that migrating lingcod had fishery exploitation rates similar to those that did not migrate. Since lingcod are highly valued, they attract commercial and/or recreational fishing in virtually every known area of concentration. The ranges in recapture rates were narrow among years (Table 2), among tagging locations (Table 3), and between sexes (Table 5), suggesting that the probability of recapture was independent of migratory behavior.

[3]H. Horton, Oregon State University, Corvallis, OR 97331, pers. commun. October 1985.

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DIGESTION RATES AND GASTRIC EVACUATION TIMES IN RELATION TO TEMPERATURE OF THE SACRAMENTO SQUAWFISH, *PTYCHOCHEILUS GRANDIS*

Squawfish, *Ptychochilus* sp., are large piscivorous cyprinids which have a reputation of being major predators on salmon and trout, although documentation for this is poor. Brown and Moyle's (1982) review on squawfish concluded that squawfish are not likely to affect salmonid populations in free flowing streams (Falter 1969; Ebel 1970; Buchanan et al. 1980, 1981), but that significant predation could occur in areas where streams are altered (dams, diversions) and in relation to fish releases.

Sacramento squawfish, *Ptychocheilus grandis*, have been reported to prey heavily on juvenile salmonids in the Sacramento River, CA, especially below Red Bluff Diversion Dam (RBDD) (Hall 1977), and have been implicated in the continuous decline of chinook salmon, *Oncorhynchus tshawytscha*, in recent decades (U.S. Bureau of Reclamation 1983, 1985). Currently governmental agencies charged with the management of anadromous fishes in California are attempting to decrease the number of squawfish in the Sacramento River, especially near RBDD. The justification for Sacramento squawfish removal is based on a report by Hall (1977). Unfortunately, the estimate of squawfish predation rates by Hall (1977) were made without knowledge of the digestion rates or gastric evacuation times of Sacramento squawfish in relation to temperature and is likely an overestimate.

Bentley and Dawley (1981) found that northern squawfish, *P. oregonensis*, consumed 14.3 g of fish per day at 10°C. Based on this estimate Sacramento squawfish below RBDD would consume only 3 or 4 salmon/day (mean size of hatchery salmon released into the Sacramento River is 4.0 to 5.0 g). This estimate is lower than the 20 salmon/day calculated by Hall (1977) for Sacramento squawfish below RBDD. The ability of predatory fish to consume prey is mediated, at least in part, by the digestion rate and the extent of gastric evacuation (Grove and Crawford 1980; Jobling and Wandsvik 1983). Several workers (Falter 1969; Steigenberger and Larkin 1974; Persson 1979, 1981, 1982; Jobling 1980; Smith 1980; Hofer et al. 1982) have shown that digestion rates in fishes increases with increasing temperature.

The purpose of this study was to determine digestive rates and time for gastric evacuation of the Sacramento squawfish in relation to temperature. Sacramento squawfish digestion rates increased with increasing temperature, while evacuation times decreased with increasing temperature.

Methods

Sacramento squawfish ($\bar{x}$ = 370 mm standard length [SL], range = 300-456 mm SL) were captured, using hook and line or a boat electrofisher, immediately below Red Bluff Diversion Dam (RBDD). The length-weight relationship for Sacramento squawfish was $Y = 4.03 + 2.66X$. Fish were transported to University of California, Davis, and treated immediately with nitrofurazone or potassium permagnate. The fish were held for several days at their capture temperature before the tem-

perature was adjusted to the experimental temperatures. The temperature was adjusted upward 1.0°C or downward 0.5°C per day until the experimental temperature was reached. Temperatures were maintained using an immersion heater and thermoregulator. Fish were then held for 14 d at the experimental temperature. Sacramento squawfish were fed mosquitofish, *Gambusia affinis*; golden shiner, *Notemigonus crysoleucas*; or threespine stickleback, *Gasterosteus aculeatus*, in excess during the holding period.

Sacramento squawfish were starved 72 h at 5° and 10°C and 48 h at 15° and 20°C prior to the digestive trials. Digestive trials were 4, 16, 32, and 48 h at 5°C; 2, 4, 8, 16, and 32 h at 10°C; 1, 2, 4, 8, and 16 h at 15°C; and 2, 6, and 10 h at 20°C.

Sacramento squawfish were force-fed juvenile chinook salmon obtained from the Coleman National Fish Hatchery (mean wet weight = 3.7 g). Each squawfish was fed four salmon because squawfish captured below RBDD in 1982 averaged approximately four salmon (x = 3.9, Vondracek et al.[1]) in their foreguts. The weight of each squawfish was estimated before a digestive trial. Each juvenile chinook salmon was weighed before the feeding trials. The salmon were selected by size to insure that each squawfish received an equivalent size adjusted ration. I attempted to feed a ration of about 2.0% of the squawfish wet weight. The mean ration actually fed was 1.8%. Squawfish were selected by size for each digestive time period to ensure an even distribution of sizes.

During force feeding Sacramento squawfish were placed into a V-shaped trough lined with polyethylene foam. Once in the trough another piece of foam was placed over the fish to restrain it. No anesthetic was used. The chinook salmon were introduced into the anterior portion of the alimentary tract of the squawfish using a large syringe (Falter 1969). The syringe (18 mm diameter) was inserted into the esophagus and past the pharyngeal teeth with the plunger removed. Once in place the salmon were introduced into the syringe. The plunger was then replaced and depressed. Groups of three to five squawfish were placed into small circular tanks maintained at the desired temperature immediately after feeding. Individual fish were identified by placing a numbered Floy[2] anchor tag between the rays of the dorsal fin.

After the prescribed digestion period Sacramento squawfish were netted from the small experimental tanks and placed into the foam-lined trough. A catheter connected to a small water pump was inserted into the anus. Digestion tract contents were flushed through the mouth and collected in a fine mesh net. The digestive tract contents were weighed (salmon were weighed individually if digested <30% and en masse if >30%) and placed in a drying oven in 60°C for 24 h. Dry weights did not change after 24 h. An initial dry weight of each ration was determined by sacrificing 5 to 10 salmon prior to the digestive trials. Mean percent dry weight of the salmon was 20.8 ± 2.0% for the 10° and 15°C trials and 21.9 ± 2.1% for the 5° and 20°C trials. If the dry weight of the digested ration exceeded the estimated initial dry weight, the percent of the ration was set to 100%. The dry weight of the digested ration exceeded the estimated initial dry weight during 17 trials with a mean of about 104%.

Digestive rates at each temperature were determined by linear regression of the percent of the ration remaining in the alimentary tract versus time after force feeding. The initial wet weights of the salmon fed to the squawfish were not used in the regression analysis. Time for alimentary tract evacuation for each temperature was assumed to be the point where the extrapolated regression for digestion intersected the x axis (time after force feeding).

Results

The digestive rates of Sacramento squawfish were directly related to temperature, while the gastric evacuation times were inversely related to temperature (Fig. 1). The digestive rates were 1.8%/h at 5°C, 2.6%/h at 10°C, 6.3%/h at 15°C, and 8.2%/h at 20°C. Gastric evacuation times were 61 h at 5°C, 38 h at 10°C, 17 h at 15°C, and 14 h at 20°C.

The digestive process appeared to involve at least two phases. During the initial phase, the wet weight of the ingested salmon increased. The duration of the initial phase was inversely related to the experimental temperature. At 5°C the initial phase was at least 16 h, 4 h in duration at 10°C, 2 h at 15°C, and approximately 2 h at 20°C. During the second phase the percent dry weight of salmon remaining in the digestive tract decreased linearly with time.

[1]Vondracek, G., S. R. Hanson, and P. B. Moyle. Sacramento squawfish, *Ptychocheilus grandis*, predation on juvenile chinook salmon, *Oncorhynchus tshawytscha*, below the Red Bluff Diversion Dam in the Sacramento River, California. Manuscr. in prep. Wildlife and Fisheries Biology, University of California, Davis, CA 95616.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries, Service, NOAA.

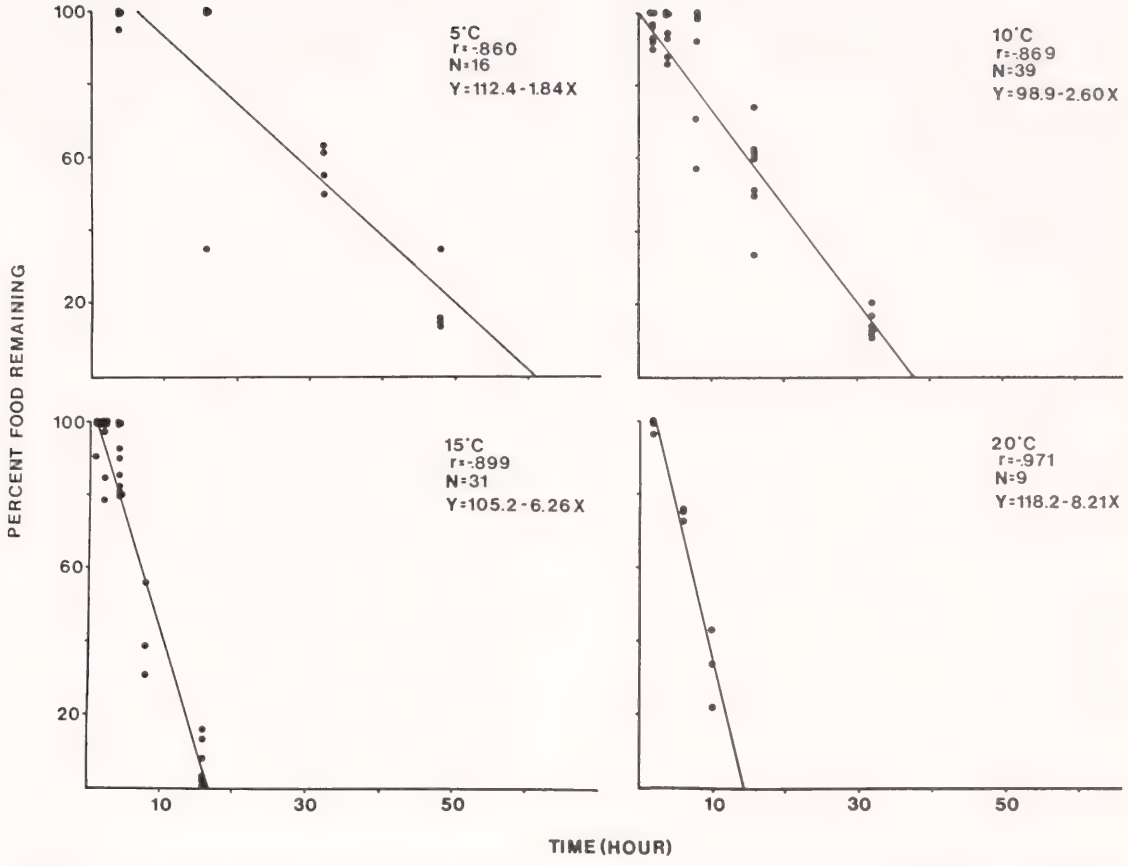

FIGURE 1.—The percent dry weight of juvenile chinook salmon remaining in the digestive tract of force-fed Sacramento squawfish after specified digestion periods at 5°, 10°, 15°, and 20°C. Each squawfish was fed four salmon.

The mean time for complete gastric evacuation over the temperature range examined can be calculated using a curvilinear equation in the form:

$$\log GE = 1.996 - 0.045T \qquad (1)$$

where GE = gastric evacuation (h)
T = temperature (°C)

Although other equations may be equally applicable, Equation (1) fits the data well ($r^2 = 0.978$, Fig. 2).

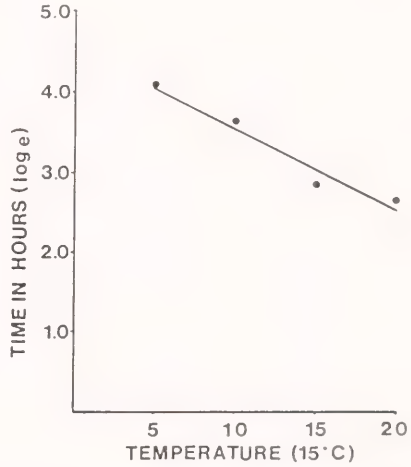

FIGURE 2.—Estimated time for complete gastric evacuation of Sacramento squawfish force-fed four juvenile chinook salmon at 5°, 10°, 15°, and 20°C.

Discussion

The digestion and gastric evacuation rates of Sacramento squawfish in relation to temperature differ in some respects than for the northern squawfish. The gastric evacuation times of the Sacramento squawfish in this study are different from the times calculated from equations presented in Falter (1969)

and Steigenberger and Larkin (1974) (Table 1); however, the times noted in this study are bracketed by the other studies. Falter's equations predict that gastric evacuation would be complete in about 29 h at 6° and 10°C and about 10 h at 16.5° and 20°C. In contrast Steigenberger and Larkin's data predict that northern squawfish would complete gastric evacuation in 84, 51, 23, and 13 h at 6°, 10°, 15°, and 20°C, respectively.

TABLE 1.—Estimated time (hours) for total evacuation of stomach contents of Sacramento squawfish held at selected temperatures.

Source	Temperature (°C)			
	6	10	15	20
Falter 1969	30	29	9 (16.5°C)	11
Steigenberger and Larkin 1974				
small	84	51	23	13
large meal	163	141	28	18
Vondracek (this study)	61 (5°C)	38	17	14

There were several differences in the protocol between the studies of Falter (1969), Steigenberger and Larkin (1974), and the present investigation which may account for the differences noted in digestion and gastric evacuation. Differences in protocol included length of acclimation period, meal size, predator size, and number of prey per meal. Falter apparently acclimated the northern squawfish in his experiments for variable time period, but not <48 h. Falter fed only one prey item at a time then sacrificed the squawfish in his studies and dissected the alimentary tract. The squawfish in Falter's study ranged from 100 to 550 mm total length. Steigenberger and Larkin (1974) used northern squawfish between 150 and 400 mm fork length, only allowed an overnight acclimation period to each temperature and also sacrificed the squawfish. In this study Sacramento squawfish (size range 300-456 mm standard length) were acclimated for at least 14 d to each temperature, fed four prey items, and then had their alimentary tracts pumped. Jobling (1981) pointed out that gastric evacuation is volume-dependent and that as the number of prey per meal increases gastric evacuation time increases.

In the present experiment digestion was linear during the second phase of the digestive process. Jobling (1981) stated that the difference between the surface-to-volume ratio between large and small food particles is important in determining the pattern of digestion. Jobling further suggested that an exponential function describes the digestive process of small, easily digested prey items, but a linear expression gave the best fit for large prey items.

The digestive rates and gastric evacuation times of the Sacramento squawfish in relation to temperature suggest that the consumption estimate of Hall (1977) of 20 juvenile salmon/day per squawfish was likely an overestimate. Water temperatures at RBDD are typically near 4.5°C in January and may increase to 10°C by late March (U.S. Bureau of Reclamation unpubl. data). Bentley and Dawley (1981) found that northern squawfish only consumed 14.3 g of fish per day at 10°C which would equal <10 fish per day even if the average size was 1.5 g. I suggest that squawfish would not consume 20 salmon/day between January and March during this period when approximately 80% of the juvenile salmon migrate downstream. As water temperatures continue to increase, predation by squawfish would likely also increase. However, juvenile salmon migrate primarily at night in the Sacramento River (Hallock and Van Woert 1954; Vondracek et al. fn. 1) which limits the predation by the visually oriented squawfish.

I suggest that the predation rate of Sacramento squawfish on juvenile salmon at RBDD is lower than previously believed because of the physiological effects of temperature on squawfish digestion during January to March.

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LABORATORY REARING OF THE SQUID *LOLIGO PEALEI* TO THE JUVENILE STAGE: GROWTH COMPARISONS WITH FISHERY DATA

The common squid of the Northwest Atlantic, *Loligo pealei* Lesueur, 1821, is a valuable species that is exploited not only as a food for human consumption, but as an important research model in biomedicine (especially for the giant axon). Summers (1983) reviewed much of the ecological and fisheries literature in his description of the life cycle of *L. pealei*. There is an important gap in our knowledge of feeding, growth, and behavior during the early phases of the life cycle. In 1980, we reported the first data from young *L. pealei* reared to 40 d posthatching (Yang et al. 1980). We now present additional data on squid reared from hatching to 6 mo and compare existing laboratory growth data with estimates from fisheries data.

Materials and Methods

The squid were reared in closed system aquaria in artificial seawater (Instant Ocean[1]). All details of system design and rearing techniques can be found in Yang et al. (1983, 1986). Wild-collected egg strands and laboratory-spawned eggs were obtained from the Marine Biological Laboratory in Woods Hole, MA and air shipped to Galveston, TX on 27 August 1985. Transit time was 30 h and the eggs were shipped in natural seawater (33 ppt). Upon arrival the water temperature was 16°C, pH 7.5, and NH_4-N 1.52 mg/L. The eggs were acclimated immediately and placed in a 1,600 L circular culture tank (CT) for incubation and early rearing. The major hatch occurred on 9 September 1985, and on 11 September (day 1 of the experiment) the spent egg capsules were removed. During this 14-d incubation

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

period water conditions were 13.8°C, 35.0 ppt, pH 8.01, and NH_4-N was <0.01 mg/L. The squid were initially fed three to seven times daily on assorted zooplankton that consisted mainly of copepods (0.5-2.5 mm body length). Subsequently, *Palaemonetes* sp. shrimp larvae, *Penaeus* sp. shrimp larvae, *Mysidopsis* sp. mysids, and fish larvae were offered. Once the squid attained 20 mm mantle length (ML), they were transferred to a 9,950 L raceway culture tank (RW) and their diet consisted of *Palaemonetes* sp. adults and small fish (*Menidia* sp.).

Results

Water quality data are listed in Table 1. Mortality was high during the first week despite many observations of active feeding by the hatchlings. The initial estimated population was 6,673 squid and 99% of these died by day 5. By day 13 only three squid were alive and these survived to days 23, 130, and 172.

TABLE 1.—Water quality of circular culture tank (CT) and raceway culture tank (RW) systems for *Loligo pealei*.

	CT system (days 1-124)	RW system (days 124-171)
Temperature (°C)		
Mean	15.8	21.3
(Range)	(13.2-19.5)	(18.2-22.9)
Salinity (ppt)		
Mean	33.8	36.1
(Range)	(33.0-35.0)	(36.0-36.5)
pH		
Mean	8.04	8.13
(Range)	(7.9-8.1)	(8.08-8.18)
Ammonia-nitrogen (mg/L)	<0.046	<0.046
Nitrite-nitrogen (mg/L)	<0.002	<0.002
Nitrate-nitrogen (mg/L)	<5.20	<16.30

The types of food organisms offered to the squid and the periods they were fed are summarized in Figure 1. From days 1 to 57, the squid were fed wild-caught zooplankton (collected near shore and in the bays near Galveston Island). The copepods *Centropages velificatus*, *Temora turbinata*, *Eucalanus pileatus*, and *Labidocera aestiva* were the predominant species in the plankton, while crab zoea, sergestid shrimps, cladocerans, chaetognaths, and fish larvae were less common. We estimate plankton density at about 40/L during this period. There was certainly ample food available and feeding (mostly on copepods) was seen often from day 1 onward. Beginning day 22, palaemonid shrimp larvae (2-4 mm) were added to the tank and captured by squid. The squid were first able to capture mysid shrimp (2-8 mm) on day 51, and by day 57 benthic crustaceans (mainly *Mysidopsis* sp.) replaced zooplankton as the main diet. During this period food organism densities fluctuated between 2 and 10/L. As late as 44 d posthatching, squid (4-5 mm ML) were still seen eating copepods (*Labidocera aestiva*) as small as 1-2 mm long even with larger crustacean food available. After the transfer to the RW system, only benthic adult palaemonid shrimp and occasionally fishes were fed (<0.15/L).

The squid hatched at a mean size of 1.84 mm ML. The largest squid lived 172 d and attained a length of 35.4 mm ML and weighed 2.77 g. This female had a nidamental gland of 5.15 mm, indicating that the

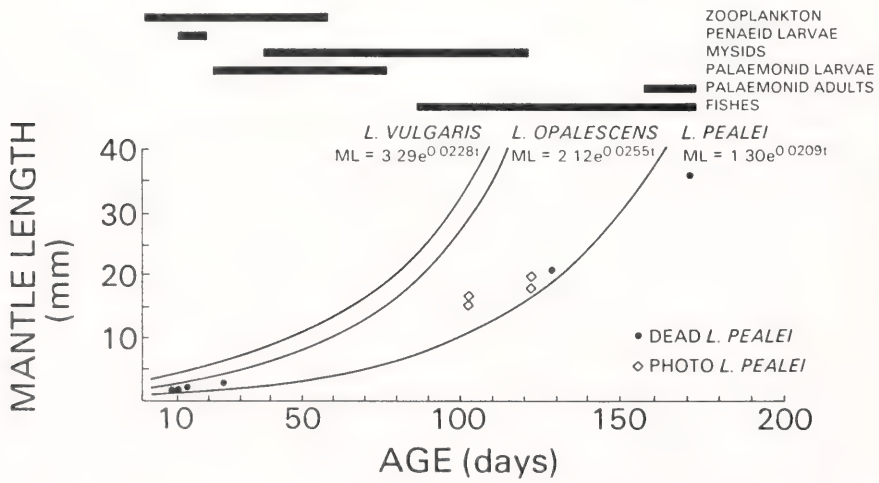

FIGURE 1.—Feeding and growth in *Loligo pealei*. Laboratory growth of *Loligo vulgaris* (Turk et al. 1985) and *L. opalescens* (Yang et al. 1986) is provided for comparison.

squid was immature but had developing gonads. Based upon 10 growth measurements (10 data points) from dead squid and several measurements obtained photographically from live squid (4 data points), the following exponential growth equation was generated for *L. pealei* (Fig. 1) during the first six months:

$$\text{Mantle length} = 1.30\, e^{0.0209t},\ r^2 = 0.98.$$

This indicates an approximate mean growth rate of 2% increase in mantle length per day.

Swimming and social behavior were observed carefully. A gentle circular flow (1-4 cm/s) was maintained in the CT system. Two squid 4 mm ML (41 d old) were able to maintain their position against a current of 1.8 cm/s. One week later (day 49), the squid could maintain their position in a current of 2.9 cm/s. On day 52, the two squid (approximately 5-8 mm ML) first showed schooling behavior by swimming parallel to one another throughout the day. They usually stayed in the darker areas of the tank but frequently moved into the lighter areas, probably to feed on the mysids that concentrated there. The final mortalities were caused by trauma and secondary infections that resulted from bumping the walls of the tank (Hulet et al. 1979).

Discussion

Since our first small-scale experiments with *Loligo pealei* (Yang et al. 1980), we have enlarged and refined our squid culture methodology enough to allow us to grow *L. forbesi* and *L. opalescens* through the life cycle (Hanlon et al. 1985; Yang et al. 1986). *Loligo pealei*, with its very small hatchling size (1.8 mm ML vs. 4.0 and 2.7, respectively for *L. forbesi* and *L. opalescens*), continues to be difficult to rear. Although our culture results in this report were poor numerically, they were a vast improvement over the many attempts in the past 100 yr to rear *L. pealei* (Verrill 1881; Williams 1909; Arnold et al. 1974). Significant improvements over our past *L. pealei* experiment include 1) increasing the culture tank size from 66 or 99 L to 1,600 L, 2) improved filtration capacity, and 3) feeding the squid many times daily (compared to twice) on different types and sizes of wild-caught zooplankton (compared to small copepods only). We cannot explain the high early mortality in the present experiment even though it is characteristic of all *Loligo* spp. rearing experiments thus far; feeding was observed often and the water quality remained in an acceptable range. Predation by wild zooplankton on squid hatchlings was possible (e.g., crab megalops), but this factor alone did not cause the high mortality. The small hatching size of *L. pealei* may partly explain the greater initial mortality (compared with *L. opalescens* and *L. forbesi*) since providing food organisms within the proper size range was more difficult. The zooplankton offered to the squid during the first week was composed primarily of copepods ranging from 0.5 to 2.5 mm long, i.e., 25 to 110% the length of the squid. Nevertheless, squid hatchlings captured and fed upon copepods, often the largest ones. Occasionally, however, hatchlings avoided copepods and appeared startled by their jerky movements. Curiously, it is this same jerky motion that provides the behavioral stimulus for all *Loligo* hatchlings to feed upon copepods. However, if enough cannot be captured by the small *L. pealei*, they may not be able to meet the high energetic costs of pursuit, capture, and digestion of a mobile, armored prey. Another possible contributor to mortality may have been reduced levels of dissolved organic nutrients in our artificial seawater (which was physically, chemically, and biologically filtered; cf. Manahan and Stephens 1983) combined with a qualitatively restricted diet compared to nature.

The value of laboratory data is its potential to verify or refute hypothesized descriptions based on limited or discontinuous fisheries data. Although the number of individuals studied was low (only two squid after day 23), several growth and behavioral patterns can be described. For example, schooling behavior, which depends partly upon size and swimming strength, was observed at a similar size for cultured *L. pealei* (4-6 mm ML, 50-60 d; this report), cultured *L. vulgaris* (5-10 mm ML, 20-40 d; Turk et al. 1986), and cultured *L. opalescens* (8-11 mm ML, 40-50 d; Yang et al. 1986). The appearance of schooling behavior may be related to the transition from the planktonic phase to the juvenile and adult demersal (neritic) phase of the life cycle. Increased swimming ability associated with schooling would allow the young squid to migrate vertically and exploit other food sources during the night. Squid size seems to be a key, with all three species first exhibiting schooling behavior when the hatchlings are 5 to 10 mm ML. Age at schooling is more variable, as early as 20 d for *L. vulgaris* (the largest hatchling) and as late as 60 d for *L. pealei* (the smallest hatchling). These observations, while limited to two individuals, conform generally to estimates of the end of the planktonic period for *L. pealei* in nature. Vecchione (1981) estimated that a distinct change in morphometric growth in *L. pealei*, especially tentacle growth, occurred at 4.5 mm ML. A change in

lifestyle at this size is confirmed further by changes in chromatophore patterns from a ventro-dorsal to a dorso-ventral patterning gradient (McConathy et al. 1980; Vecchione 1981). Estimates based upon field data (Summers 1968, 1983; Vecchione 1981; Table 2) put the age of transition at <1 mo.

TABLE 2.—Growth rate comparisons for young *Loligo pealei*.

Species	Growth rate (mm/mo)	Mantle length increase (mm)	Temp. (°C)	Reference
Field				
L. pealei	28-46	2 to 30-48	15-19	Verrill 1881
L. pealei	14-18	2 to 70-90	—	Verrill 1881
L. pealei	9-14	2 to 62-100	8-15	Verrill 1881
L. pealei	11-28	2 to 45-110	?-19	Summers 1968
L. pealei	17-20	2 to 70-90	—	Mesnil 1977
L. pealei	36	2 to 40	10-24	Vecchione 1981
L. pealei	24	2 to 4	17-23	Harrigan 1985
Laboratory				
L. pealei	4-6	2 to 35	13-23	this report
L. vulgaris	19	3 to 75	12-23	Turk et al. 1985
L. opalescens	13	3 to 44	15-16	Yang et al. 1986

Growth of laboratory-reared *Loligo pealei* (Fig. 1) was slower than that of either *L. vulgaris* (Turk et al. 1986) or *L. opalescens* (Yang et al. 1986) reared in similar tanks at slightly colder temperatures. Growth of *L. pealei* in our previous culture experiment (Yang et al. 1980) was 3.1 mm ML at 40 d, and this datum fits with Figure 1 and the growth curve. Daily growth rate estimates (derived from the instantaneous growth rates) were 2.28%/day for *L. vulgaris*, 2.55%/day for *L. opalescens*, and 2.09%/day for *L. pealei*. Table 2 compares the published estimates of growth rate in *L. pealei*. It is clear that estimates from field samples are far higher than our laboratory results of 4-6 mm/month with *L. pealei* (temperatures are generally comparable). The fastest growth rates we have measured in laboratory-reared squid during the first three months have been 19 mm/month in *L. vulgaris* and 13 mm/month in *L. opalescens* (mean rates are closer to 7 and 6 mm/month, respectively). Extrapolating these data in either direction (field vs. laboratory) is difficult because growth rates must be calculated over short periods (i.e., <1 mo) and under similar circumstances to be compared directly. Our laboratory results with *L. pealei* are probably low estimates compared with its growth rate in nature; they are low compared even with *L. vulgaris* and *L. opalescens* grown in our laboratory. However, since growth is clearly exponential in form in these three squid species as well as other cephalopods (Forsythe and Van Heukelem in press), the numerical value of growth rate in millimeters per month will increase disproportionally fast as the animal gets larger; thus the *L. pealei* data extrapolated to 60 or 90 mm ML would compare more favorably with most other growth estimates in Table 2. The growth rate estimates of Vecchione (1981), Harrigan (1985), and the first estimate by Verrill (1881), all based upon size-frequency data, seem to be excessive in view of laboratory and field growth data on cephalopods (Forsythe and Van Heukelem in press). Based upon our rearing experience with *Loligo* spp., we estimate that *L. pealei* in nature could grow as fast as 20 mm/month during the first few months if conditions were optimal.

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CHANGES IN THE POPULATION STRUCTURE OF MALE STRIPED BASS, *MORONE SAXATILIS*, SPAWNING IN THE THREE AREAS OF THE CHESAPEAKE BAY FROM 1984 TO 1986

The striped bass, *Morone saxatilis*, supported important commercial and recreational fisheries until recently. Population declines over the past 15 years have prompted fishing restrictions in most states along the Atlantic coast of the United States and a complete moratorium in Maryland. Spawning success of *M. saxatilis* has been poor since 1970, except for 1982 when the juvenile index reported by the Maryland Department of Natural Resources which was near the 50-yr average for Chesapeake stocks (Boone and Uphoff 1983).

Knowledge of the population structure of the striped bass is important to restoration efforts. Many attempts have been made to identify distinct stocks along the Atlantic coast and within Chesapeake Bay. Morphological studies have found evidence of discrete stocks within the Chesapeake system (c.f. Setzler et al. 1980 for review), while studies of allozyme variation have been ambiguous (Morgan et al. 1973; Grove et al. 1976; Sidell et al. 1980). Electrophoretic studies have found only limited allozyme variation and, thus, discrimination of stocks has been problematical. To further understand the reproductive patterns of striped bass in the Chesapeake Bay, an analysis of mitochondrial DNA (mtDNA) genotypes among spawning individuals was initiated in 1984. For the most part, mtDNA is maternally inherited and and provides information concerning matriarchal ancestry. The results of this analysis for the overall striped bass fishery will be reported elsewhere, but support the conclusion that distinct stocks exist in the Chesapeake Bay. As part of this survey, it was deemed important to examine the distribution of mtDNA genotypes of striped bass among 1982 year class individuals as they recruited into reproducing populations and to determine if the distribution of these genotypes changed in subsequent years. I report here on the distribution of mtDNA genotypes in 1982 year class males during their first (1984) and third spawning seasons (1986).

Methods

Striped bass were gill netted from the Chesapeake Bay at the mouth of the Sassafras River (Worton Point, 23, 24, 26 April 1984 and 7, 9 May 1986), the Potomac River (2 May 1984 and 29 April 1986) and Choptank River (9 May 1984 and 13 May 1986) during the spawning season. Age and sex determinations were made by counting scale annuli and visually inspecting the gonads, respectively. The accuracy of scale annuli for aging striped bass was reviewed by Setzler et al (1980). MtDNA was isolated from the livers according to the methods of Chapman and Powers (1984) and digested with the restriction endonucleases *Hind* III, *Eco* RI, and *Bcl* I. The digested mtDNA fragments were separated on 0.8% agarose gels. To insure consistent scoring of genotypes, 1984 samples were rerun against 1986 samples. Homogeneity of mtDNA frequencies within localities and among years was tested by G^2 tests with pooling of expected classes less than five (c.f. Sokal and Rolf 1969).

Results and Discussion

Variation in *M. saxatilis* mtDNA was characterized by fragment length polymorphisms that can be

divided into 14 distinct matriarchal clones. For this report, I consider only the five mtDNA size groups that account for more than 95% of the variation in Chesapeake Bay specimens. Molecular weight estimates for the size groups (Fig. 1) were A = 17.5 kilobases (kb), B = 17.6 kg, C = 17.7 kb, D/E = 17.65/17.75, and F = 17.8. The D/E genotype indicated individuals with two distinct molecules. These genotypes were easily distinguished by the migration of the lowest molecular weight fragment produced by digestion with the enzymes mentioned above.

The distribution of mtDNA genotypes in males taken from each of the collecting localities changed dramatically from 1984 to 1986 (Table 1). In 1984, the B genotype was found in more than 75% of the specimens (81% in the Potomac, 53% in the Choptank, and 100% in the Worton Point area). In 1986 this genotype represented about 30% of the spawning 1982 year class males (21% in the Potomac, 23% in the Choptank, and 42% in the Worton Point area). The C genotype represented 15% of the specimens in 1984, but was more common in 1986 (49%). The D/E and F genotypes were not observed in 1984, but combined to represent 17% of the specimens taken in 1986. The changes in mtDNA genotype frequencies from 1984 to 1986 are highly significant in the combined data and in the Worton Point and Potomac spawning areas (Table 1). The nonsignificant result in the Choptank may be due to the effects of pooling and inadequate sample size.

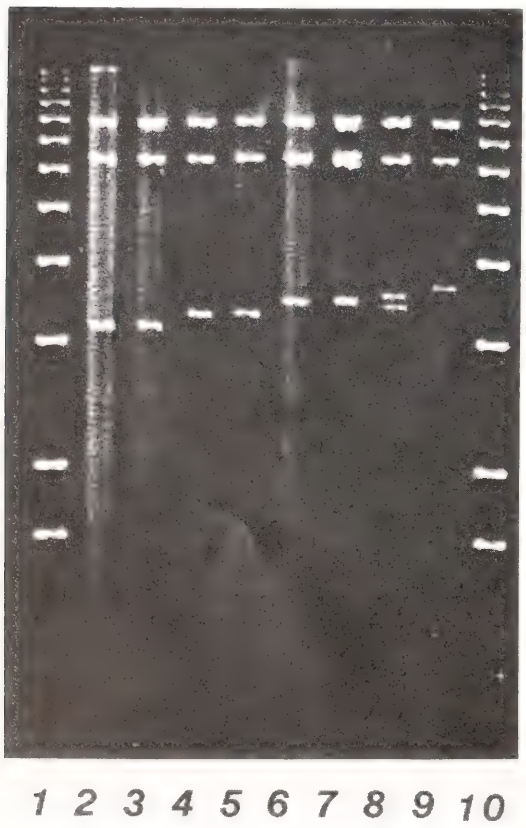

FIGURE 1.—*BclI* digestion patterns of *Morone saxatilis* mtDNA showing size fragment variation for genotypes A = 17.5 kg, lanes 2, 3; B = 17.6 kb, lanes 4, 5; C = 17.7 kb, lanes 6, 7; D/E = 17.65/17.75, lane 8; and F = 17.8 kb, lane 9. Lanes 1 and 10 are 1 kb ladder standards purchased from BRL, Inc. (Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.)

Year to year variation in the frequencies of various mtDNA genotypes found among spawning individuals could arise from changes in the age composition. Previously spawning individuals may die and new recruits may be descendants of different females. These possibilities are not concerns here because data are reported only upon the 1982 year class males. The changes in mtDNA frequencies within spawning members of this group can be explained by either of three hypotheses. First, the abundance of B genotypes in the 1984 sample may be an overestimation of their actual frequency, but the age at which male striped bass join spawning aggregations may depend upon genetic factors that are marked by (or perhaps linked to) mtDNA genotypes. As the remaining genotypes became sexually mature, mtDNA frequencies among spawners more accurately reflected the frequencies in the 1982 year class. Second, the 1984 data may actually reflect genotype frequencies during that year, but differential mortalities from 1984 to 1986 substantially altered the frequencies. This does not necessarily imply selective mortalities because aggregations of B genotypes following the spawning season may have been more susceptible to fishing pressure. Third, the increase in the C, D/E, and F genotypes may be the result of migration from other areas. The survey of Chapman and Powers (unpubl. data) did not find significant concentrations of these genotypes in the Chesapeake Bay, but this survey did not include the York and James Rivers in the Chesapeake Bay or the Hudson River. If these rivers are the source of most of the C, D/E, and F genotypes found in this study, it would require a migration rate of 50% among Chesapeake Bay and/or the Hudson River stocks to produce the frequency changes noted here.

Migratory patterns of *M. saxatilis* vary from region to region along the Atlantic coast. Populations from southern North Carolina to the St. John's River, FL, are essentially riverine and do not under-

TABLE 1.—The distribution of mtDNA genotypes and G^2 tests (Sokal and Rohlf 1969) for random distributions in the Potomac River, the Choptank River and the Worton Point area in 1984 and 1986. The expected values are in parentheses.

		Genotype					
		A	B	C	D/E	F	G^2
Potomac	1984		13 (6.9)	3 (7.2)	0 (0.7)	0 (1.1)	7.12 $P < 0.01$
	1986		6 (12.1)	17 (12.7)	2 (1.2)	3 (1.9)	
Choptank	1984	3 (1.5)	7 (5.5)	3 (4.0)	0 (1.0)	0 (1.0)	2.85 $0.1 > P > 0.05$
	1986	0 (1.5)	3 (5.5)	6 (4.0)	2 (1.0)	2 (1.0)	
Worton Point	1984	0 (0.5)	11 (6.2)	0 (3.4)		0 (0.8)	10.51 $P < 0.01$
	1986	2 (1.4)	12 (15.8)	11 (8.6)		3 (2.2)	
Combined	1984	3 (1.8)	31 (18.7)	6 (14.7)	0 (1.5)	0 (3.9)	26.62 $P < 0.01$
	1986	2 (3.1)	21 (32.3)	34 (25.3)	4 (2.5)	8 (5.1)	

take coastal migrations (c.f. Setzler et al. 1980). In the Chesapeake Bay and Hudson River, tagging studies suggest that individuals less than age 2 do not migrate extensively from their natal tributaries (c.f. Setzler et al. 1980). After this sedentary period, females begin to leave the Chesapeake Bay for coastal waters and virtually all females older than age 4 return only to spawn (Kohlenstein 1980). Females do not mature sexually until age 3 at the earliest and most do not mature until age 4 or 5 (Jones et al. 1977). In contrast, few males leave the Chesapeake Bay until age 4 or 5 and virtually all age 2 are sexually mature. Tagging studies by Manseuti (1961) suggest that larger males (ages 3-4) moved greater distances within the Chesapeake than small males (ages 0-2). Massman and Pacheco (1961) supported this conclusion and also found that James and York River fish tended to migrate northward in the bay proper. These migration studies fit nicely with the data presented here, if indeed the changes in mtDNA frequencies were due to immigration from the James and York Rivers.

Further study of striped bass population dynamics are needed to test the hypotheses outlined above. Of particular importance will be an assessment of populations from the James and York Rivers. Whatever the outcome, the data presented here will need to be considered in management plans for this economically important species.

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Text footnotes should be typed separately from the text.

Figures and **tables,** with their legends and headings, should be self-explanatory, not requiring reference to the text. Their placement should be indicated in the right-hand margin of the manuscript.

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VALIDATION OF THE OTOLITH INCREMENT AGING TECHNIQUE FOR STRIPED BASS, *MORONE SAXATILIS*, LARVAE REARED UNDER SUBOPTIMAL FEEDING CONDITIONS

CYNTHIA JONES[1] AND EDWARD B. BROTHERS[2]

ABSTRACT

Striped bass, *Morone saxatilis*, larvae were reared in the laboratory for 97 days to validate the otolith increment aging technique for this species. Otolith-increment deposition rates were determined under optimal laboratory conditions for growth and under three conditions of restricted feeding and using both light and scanning electron microscopy (SEM). Under optimal laboratory conditions, increments were deposited daily from the fourth day after hatching through the first 2 months of life and were discernible with the light microscope. For larvae reared under restricted feeding regimes and readings done with the light microscope, counts did not reflect true age. Counts obtained from these same otoliths using SEM, however, more closely reflected true daily age. Results indicate that the use of light microscopy alone can result in inaccurate estimation of age for larvae that have experienced starvation episodes.

When otolith increments in larval fish are deposited daily, with a known time of onset, precise age of each individual can be determined and the growth curves for the individuals may be generated. The ability to follow changes in growth of individuals and populations on as fine a scale as, say, a week may provide a means to improved understanding of the effects which environmental factors have on survival.

To apply this aging technique to larval striped bass, *Morone saxatilis*, daily deposition of increments and the age at first increment deposition had to be confirmed in the laboratory with known-age larvae. Although daily depositional rates of otolith increments in known-age larval striped bass have not been previously reported, daily deposition has been noted for larvae and juveniles of 17 other species of fish reared in the laboratory (see Jones 1985 for review). Nonvalidated data exist to support the concept of daily increment deposition for field-captured striped bass (Brothers et al. 1976). However, tests of depositional rate under suboptimal laboratory conditions, using light microscopy, have shown that depositional rates can be affected by the specific growth rate (Geffen 1982), by photoperiod (Radtke 1978), by food supply (Geffen 1982; Neilson and Geen 1982), and by temperature (Brothers 1978; Geffen 1983). Campana and Neilson (1985) stated that "few workers have critically assessed the assumptions upon which the age and growth inferences are based or considered the potential for environmental modification of microstructural features."

Of particular importance is the potential for counting fewer otolith increments when otolith growth rate is slowed to the extent that increments being deposited are too narrow to resolve with a light microscope. Inadequate resolution with the light microscope could lead to systematically low increment counts and thus, result in overestimation of the growth and mortality rates, and underestimation of variance in growth, all of which have important biological implications. Hence, to demonstrate that striped bass larvae from the field could be aged accurately by the otolith increment technique, we found it necessary to determine the regularity and readability of otolith-increment deposition under simulated laboratory suboptimal field conditions.

Lack of scanning electron microscopy (SEM) validation hinders the resolution of an important issue: Is daily formation of increments a robust biological rhythm common to most teleosts which requires serious and prolonged starvation to disrupt, or is it a more volatile physiological connection in which daily formation occurs only under optimal food concentrations as certain laboratory studies indicate?

Factors which affect growth and survival of striped bass larvae have been studied extensively (see Westin and Rogers 1978 for review). Rogers (1978) raised larval striped bass under various temperature and feeding regimes to determine growth under laboratory conditions. Larvae grew well at

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temperatures between 16° and 22°C and with a minimum of 1,000-2,000 *Artemia* nauplii/L. The optimum salinity range was between 3.5 and 14.0‰ (Bayless 1972). Davies (1973) studied larval survival under combinations of temperature, pH, and dissolved solids. Optimum temperature was 17.0°C; optimum pH, 7.5. Eldridge et al. (1981) studied the growth of larvae under various feeding regimes and found growth rates which approximated field growth rates at concentrations of 5,000 *Artemia*/L. They found that the "point of no return" was ill defined and starved larvae could live for as long as 31 days. Dey (1981) has reported on growth and survival of wild larvae, using length and developmental stage to estimate growth. He found growth was temperature dependent and temperatures between 12° and 15°C resulted in massive mortalities.

The purpose of this study was to determine the relationship between age, environmental condition, and otolith increment depositional rates in laboratory-raised striped bass larvae. This was accomplished by studying the increments of known-age larvae reared under both optimal laboratory conditions and restricted feeding regimes (laboratory-simulated suboptimal field conditions). Larvae were subjected to various periods of food deprivation to determine the potential dependence of increment depositional rates on nutritional condition. Specifically, incremental counts made with light microscopy and SEM were compared to evaluate the reality of apparent interruptions of daily deposition.

METHODS

Striped bass eggs were obtained from the Verplank Hatchery, Verplank, NY, within 24 hours of fertilization. Eggs were held in water obtained at the hatchery (0‰ salinity) at 18°C, under a 14L: 10D photoperiod. Light levels were 25-31 μ Einsteins/m^2 per second. This light level is approximately equal to light at a depth of 2-3 m in a coastal stream or 1 m in a coastal estuary depending on turbidity and season of the year. Eggs hatched within 24 hours of fertilization. Newly hatched larvae were transferred to 4 L jars and stocked at densities of 50 per liter. Over the first 8 days, salinities were gradually raised to 5‰ by adding filtered seawater with 0‰ water. Seventy-six days after hatching of the larvae, salinities were gradually raised to 10‰ over a span of 8 days. Water was changed at least every other day.

Four feeding conditions were established. The food for all conditions was newly hatched brine shrimp, *Artemia*. Larvae were fed ad libitum (condition 1), other larvae were starved throughout the experiment (condition 2), and other larvae were starved for the first 15 days after hatching, then fed ad libitum (condition 3). Condition 4 consisted of larvae that were intermittently deprived of food. These larvae were not fed between 39-43, 51-55, and 62-66 days after hatching, for a total of 15 days out of the 68 days they were reared. For the remaining time they were fed ad libitum.

Larvae were sampled according to the schedule listed in Table 1. Larvae that were sampled were anesthetized with Tricaine methanesulfonate (Cresent Research Chemical[3]) and sacrificed. Total length was measured to the nearest 0.1 mm. Otoliths were teased from the otic capsules with fine dissecting needles, cleared of tissue, washed in deionized water and transferred with a micropipette or with fine dissecting needles to a labeled microscope slide.

Small otoliths were mounted permanently in *Euparol* without grinding. Larger otoliths were mounted in Flowtex (Lerner Laboratories), ground with 600 grit sandpaper and read with the light microscope. A subsample of ground otoliths was removed from the Flowtex, mounted in Spurr's medium, and ground to the core on Beuhler lapidary wheels. Initial grinding on the wheels began at 180

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Sample size at age of striped bass larvae reared under four feeding regimes. N.T. = not taken.

Age (d)	Feeding regime condition			
	Continuously fed	Starved	Starved then fed	Intermittent starved
3	3			
4	8	5		
5	5	3		
6	5	5		
7	5	5		
8	5	5		
9	5	5		
10	5	5		
14	5	5		
18	5	5	2	
22	5	5	2	2
26	5	6	2	2
33	5		2	2
38	4		N.T.	N.T.
40	2		3	2
47	5		2	2
54	5		2	2
58	1		N.T.	N.T.
64	N.T.		1	N.T.
68	3		3	2
97	5		2	

grit and final polishing was done with 0.25 μm diamond paste. These otoliths were etched with 0.02N HCl, then mounted on SEM stubs and sputter coated with gold/palladium.

Three light microscopes were used: a Zeiss, a Leitz, and an Olympus. The latter two were equipped with video viewing systems and polarized light sources. Readings were done with brightfield illumination at 400, 540, and 1,000 power. Video increased magnification to a maximum of 2700×. The maximum resolution for the light microscopes was 0.5-1.0 μm. The SEM employed was a JOEL (JSM 200) equipped with both secondary electron image (SEI) and backscattered electron image (BEI) collectors.

For light microscopy, slides were chosen at random and read double blind (age of the larvae and condition were unknown). Readings were done three times for each slide. Each slide was counted only once during each session so that replicate counts did not immediately follow each other. Thirteen of the twenty-four samples from conditions 3 and 4 were used for SEM analysis. For SEM examinations, counts were blind (ages of the larvae were unknown); condition, however, was selected by the investigators to check the accuracy of the light microscope counts for conditions 3 and 4.

RESULTS

Light Microscopy

The relationship between the number of otolith increments and age, in days, for the four experimental conditions is shown in Figure 1. Fully fed larvae (n = 63), condition 1, had a regression slope of 0.98 increments/day, and the smallest standard error (Table 2). Its confidence interval included 1 increment/day. Beyond 68 days of age sagittae became very difficult to read. Continuous counting paths or an appropriate series of transects were difficult to find because the sagitta changes shape and develops new centers of deposition around the periphery of the otolith. This resulted in underestimates of true age (Table 2) for larvae older than 2 months of age.

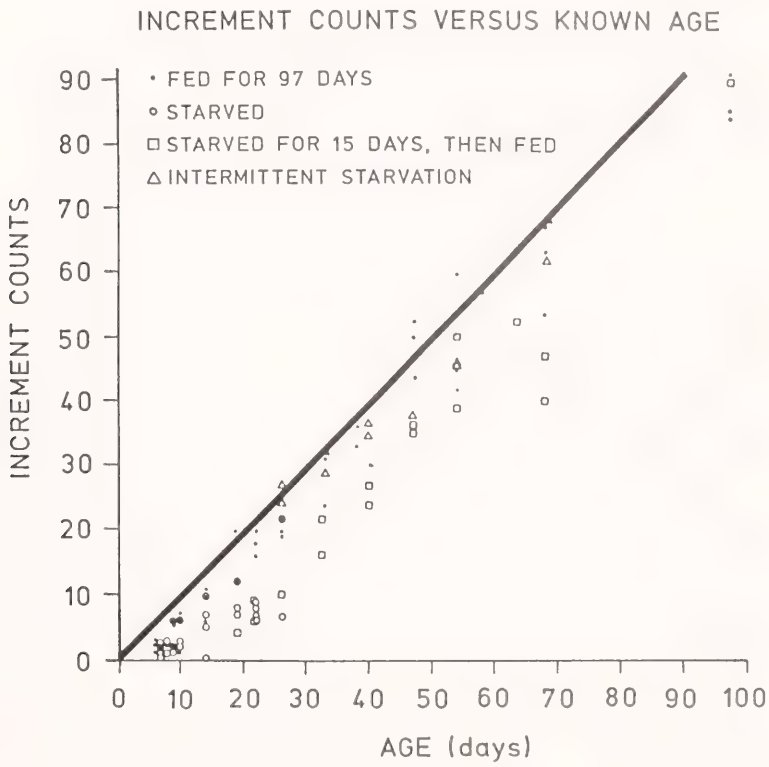

FIGURE 1.—Relationship between otolith increment count in larval striped bass and true age for four feeding regimes, light microscope observations.

TABLE 2.—Parameters for weighted regressions of increment counts on days from hatch of striped bass larvae reared under four feeding regimes. SE indicates standard error of the estimate, C.I. indicates confidence interval, N.S. indicates slope not significantly different than 1.0, * indicates $P = 0.05$.

Age	Condition	N	Slope (counts/d)	SE (slope)	95% C.I. Low	95% C.I. High	Intercept Counts	SE (int)	r^2	$P > 0.05$
68 d and younger	1 Always fed	60	0.980	0.0243	0.931	1.029	−4.016	0.4482	0.96	N.S.
All ages	1 Always fed	63	0.946	0.0169	0.912	0.980	−3.627	0.4068	0.96	*
	2 Starved	43	0.469	0.0402	0.388	0.550	−1.697	0.4325	0.77	*
	3 Starved/fed	12	0.930	0.1005	0.711	1.149	−10.430	4.3906	0.90	N.S.
	4 Intermittent	12	0.873	0.0586	0.745	1.000	2.579	2.4010	0.96	N.S.

The slope of the regression line for starved larvae (condition 2, $n = 43$), 0.469 increments/day, differed significantly from 1.0 increment/day. Increments appeared regularly spaced. Otoliths of starved larvae did not appear aberrant under the light microscope.

The regression of increment counts versus true daily age for larvae, which were starved then fed (condition 3, $n = 12$), had a slope of 0.930 increments/day with confidence intervals which included 1.000 increments/day (Table 2). However, the regression intercept was −10.430, an overestimate of age at first increment deposition. This leads to a 6-d underestimate of true age because depositional rates were underestimated during the first 2 weeks of life.

The slope of the regression line for intermittently starved larvae (condition 4, $n = 12$) was 0.873 increments/day. The slope of 1.0 increment/day fell at the very edge of the confidence interval. If a slightly smaller alpha level had been chosen, deposition would not have been assumed daily.

Initial increment formation began at 4 days after hatching with a 95% confidence interval that ranged from 3 to 5 days. Yolk-sac absorption occurs at 7 days after hatching at 18°C and first feeding begins at approximately the same time. However, initial increment deposition does not appear to be connected to these events. Two or three weakly defined increments were observed within the core in many SEM preparations. They were not counted in light or SEM readings.

Scanning Electron Microscopy

Results from the SEM study are qualitative rather than quantitative due to the small sample sizes, $n = 13$, used for the SEM. With SEM, otolith increment counts for condition 3, larvae which were starved then fed (Table 3), and for condition 4, larvae which were intermittently starved (Table 4), yielded more accurate counts than those obtained on the same specimens with light microscopy. With light microscopy counts from larvae which were starved for 15 days resulted in an underestimate of true age by 10 days (Table 3). The variability was also high (SE = 7.9 days). SEM counts underestimated true age by 2 days. Variability was small; the standard error was 3.4 and 4.0 days for SEI and

TABLE 3.—Counting bias for larvae starved for the first 15 days after hatch (calculated as estimated age − true age[1]). Underestimate of age is indicated by −; overestimate indicated by +. SEI = secondary electron image; BEI = backscattered electron image.

Sample no.	Age (d)	Microscopic technique Light	SEI	BEI
1	68	−17	0	+1
2	47	− 7	−5	−5
3	54	0	−5	−6
4	68	−24	−5	−5
5	33	− 7	+4	+5
6	47	− 8	−2	−2
7	47	− 7	−1	0
Mean bias		−10	−2	−2
SE		7.9	3.4	4.0

[1]Estimated age = number of increments + mean age at first increment formation.

TABLE 4.—Counting bias for larvae intermittently starved (calculated as estimated age − true age[1]). Underestimate of age is indicated by −; overestimate indicated by +. SEI = secondary electron image; BEI = backscattered image.

Sample no.	Age (d)	Microscopic technique Light	SEI	BEI
8	68	+ 2	−5	−6
9	47	− 5	−5	−3
10	54	−11	−1	−2
11	54	− 4	−4	0
12	47	+ 2	−4	−4
13	47	− 5	+1	+1
Mean bias		− 4	−3	−2
SE		4.9	2.4	2.6

[1]Estimated age = number of increments + mean age at first increment formation.

BEI, respectively. Light microscope-counted increments of intermittently starved larvae underestimated age by 4 days (Table 4). The standard error of the mean was 4.9 days. For this sample, both SEM techniques also gave more accurate age estimates. SEI underestimated age by 3 days (SE = 2.4 days), and BEI underestimated age by 2 days (SE = 2.6 days).

The comparison between SEI and BEI showed no significant difference in accuracy (Tables 3, 4). Figures 2A and 2B illustrate the increment structure observed with these two methods of SEM. BEI

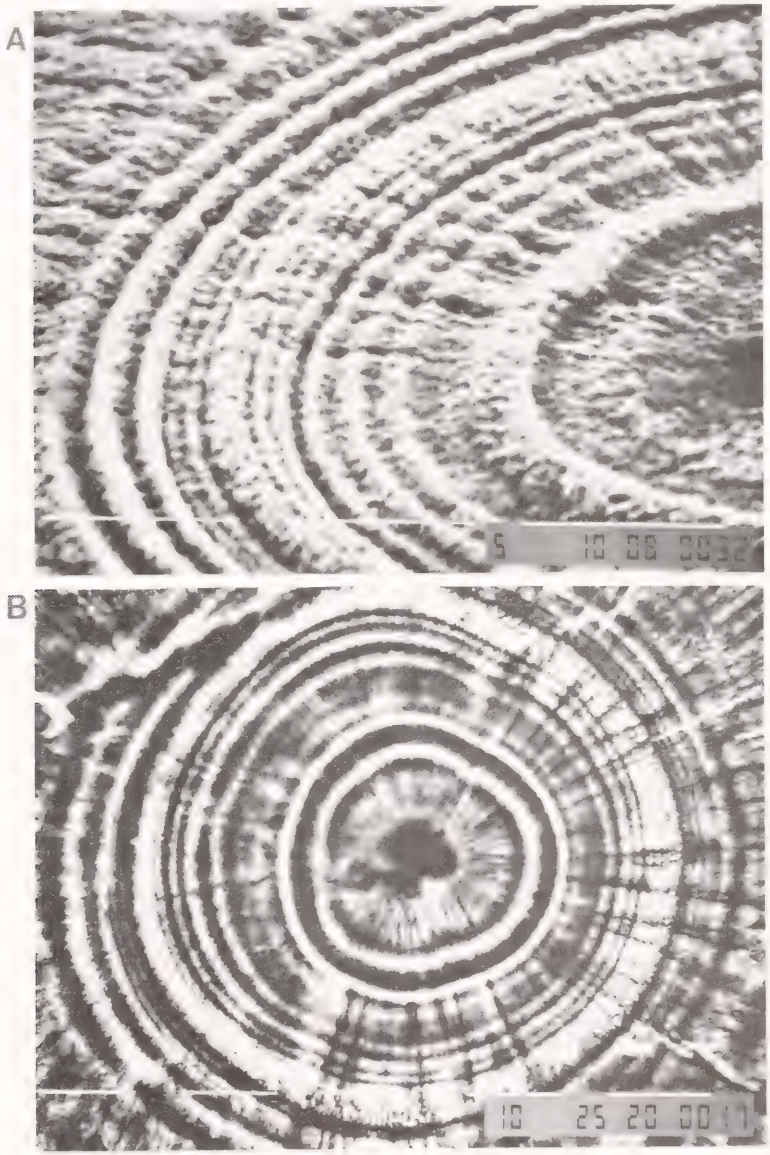

FIGURE 2.—Comparison of otoliths of larval striped bass using two scanning electron microscope (SEM), techniques. A) Normal secondary emission (SEI) photomicrograph of an otolith of a larva starved for the first 15 days posthatch then fed ad libitum until sacrificed. Increment width during starvation is approximately 5 μm. B) Backscattered emission (BEI) photomicrograph for a comparable otolith to A above. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

enhances contrast, but does not allow the specimen to be tilted. With SEI, tilting can increase increment relief and visibility.

Increments deposited during starvation were only 0.5 μm in width, too closely spaced to be discerned with the light microscope (Fig. 3). Additionally, the material that is deposited appears to be more homogenous in density, probably containing a lower amount of matrix. When etched, less material was dissolved in the area corresponding to starvation periods. This resulted in a higher area of relief, forming a broad ridgelike structure, subdivided into finer increments. The etching properties were, therefore, different compared to the same area in the otolith of a fed larvae. This ridgelike structure consistently indicated periods of starvation during the first 2 weeks of life. Ridges were not apparent for older larvae starved for shorter time intervals (Fig. 4).

DISCUSSION

Estimation of age obtained using the light microscope was not always accurate. When larvae grew well, the light microscope gave correct age estimates. However, otoliths of larvae reared under suboptimal feeding conditions gave underestimates of true age. Age estimates were more accurate using SEM, and starvation episodes were easier to recognize in the otoliths.

Light microscopy has been routinely used to estimate age in field-captured larval fish (Jones 1985). Only a few investigators have employed SEM. Although SEM improves the accuracy of age estimates, it is more costly, requires more precise preparation, and is more time consuming. However, for larvae as resistant to starvation as striped bass, SEM verification of age estimation obtained with the light microscope is necessary. In our view, investigators using increments to estimate growth should check their results from the light microscope with SEM studies. SEM analysis could be performed on a randomly chosen subsample of otoliths. If problems were uncovered, a more extensive analysis using SEM could be undertaken. Checks on a random sample using SEM are particularly important for field studies where application of the otolith increment technique to estimate field growth is relatively new.

It could be argued that larvae which undergo periods of starvation are more vulnerable to predation and may occur only infrequently in samples. Although this is quite likely, it is precisely during

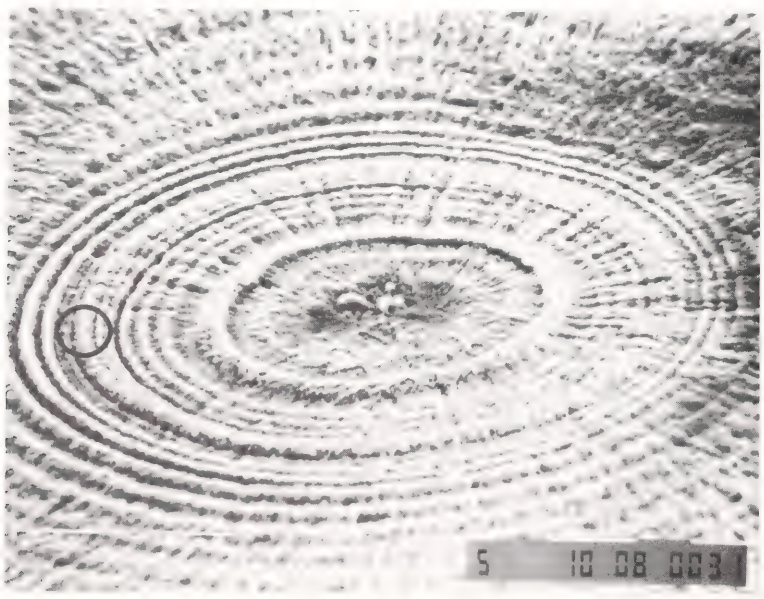

FIGURE 3.—SEM photomicrograph of an otolith of a larva starved for the first 15 days of life then fed ad libitum. A ridge, indicated by the circle, develops as the result of etching the otolith with 0.02 N HCl. This ridge corresponds to the period of starvation. Increment width during starvation is approximately 5 μm. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

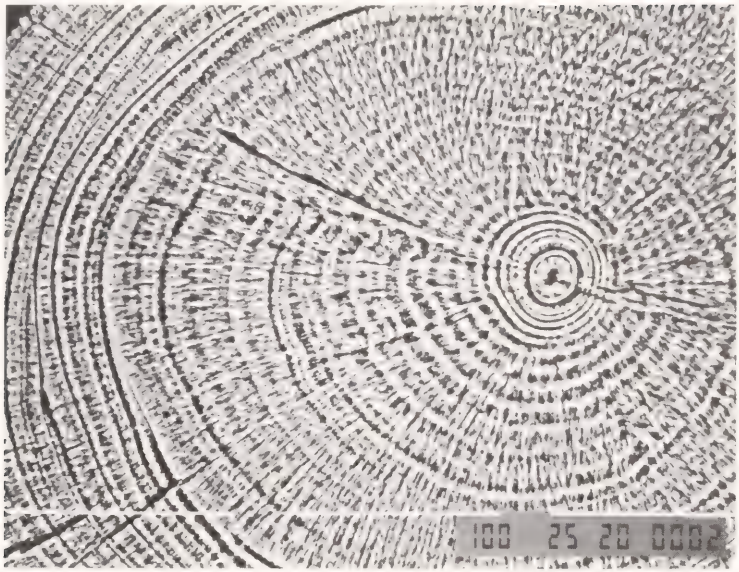

FIGURE 4.—SEM photomicrograph of an otolith of an intermittently starved larva. Note the pattern of narrow bands, indicated by the bracket, typical of starvation episodes. Increment width during starvation is approximately 5 μm. Legends in the micrographs indicate 1) length of scale bars in μm, 2) accelerating voltage KV, 3) mm working distance, 4) coded photo number.

years that have poor conditions, hence poor recruitment, that good age-based growth and mortality estimation would be the most useful. During such years, more of the young larvae could have their true age underestimated. This would result in overestimation of the abundance of younger larvae and therefore a steepened mortality curve. The best approach for routine field work may be to incorporate a design in which a small subsample of otoliths are analyzed by SEM to test for bias using the light microscope.

Bias in light microscope counts may account for the less-than-daily otolith increment deposition that has been demonstrated in the laboratory (Geffen 1982). For field-captured fish, there is no way of knowing whether light microscope counts are biased without the use of SEM. Additionally, this potential bias affects the variance of the estimate of size-at-age. When larval age is underestimated, under conditions which have resulted from poor growth, the variance is improperly decreased for young fish. Hence, lower variances may be a product of both high mortality and bias in age estimation.

Finally, the light microscope biases are more important for young larvae. By simple arithmetic, a bias of 3 days in a 7-d-old fish will result in a far more inflated growth rate than will a bias of 3 days (or for that matter 10 days) in a 60-d-old fish. The growth rate of the younger fish will be inflated 1.75 times compared with only 1.05 times (or 1.2 times using the 10-d bias) for the older fish.

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OPTIMUM ALLOCATION FOR ESTIMATING AGE COMPOSITION USING AGE-LENGTH KEY

HAN-LIN LAI[1]

ABSTRACT

A new optimum allocation method for age-length keys (ALK) was developed by applying Kimura's Vartot, an error index of estimated age composition. The method is applied to Pacific cod, sablefish, and walleye pollock. At the present working capacity, the total of 10,000 minutes (about 70 working days) will approximate the most effective cost to estimate age composition for the three species. Increasing costs beyond this level will show no more gain.

Age-length keys (ALK) are widely used for estimating age compositions in fisheries. The theory of ALK is based on a double sampling technique with stratification (Tanaka 1953). The first stage involves a simple random sampling for a relatively large size, less costly length sample. The second stage involves a stratified random sampling for a smaller size, more costly age subsample from each length stratum. Following the approximation of Kutkuhn (1963) and Southward (1963), the proportion of fish at the ith age class (p_i) and variance of p_i are estimated as

$$p_i = \sum_{j=1}^{L} l_j q_{ij} \quad (1)$$

$$\mathrm{Var}(p_i) = \sum_{j=1}^{L} \left[\frac{l_j^2 q_{ij}(1 - q_{ij})}{n_j} + \frac{l_j (q_{ij} - p_i)^2}{N} \right] \quad (2)$$

where l_j is the proportion of fish that fall into the jth length stratum,
N is total length sample size,
n_j is the size of age subsample in the jth length stratum,
q_{ij} is the proportion of n_j fish classified into the ith age class,
A is the number of age classes, and
L is the number of length strata.

Kimura (1977) defined Vartot as the sum of all variances of the p_i:

$$\mathrm{Vartot} = \sum_{i=1}^{A} \mathrm{Var}(p_i) = E\left[\sum_{i=1}^{A} (\hat{p}_i - p_i)^2 \right] \quad (3)$$

which is an error index for assessing precision of the ALK. Furthermore, Vartot is the expectation of the squared distance between the estimated age composition $\hat{P}' = (\hat{p}_1, \hat{p}_2, \ldots, \hat{p}_A)$ and the true age composition of the population $P' = (p_1, p_2, \ldots, p_A)$. Then, $D = \sqrt{\mathrm{Vartot}}$ can be interpreted as a kind of average Euclidean distance between $\hat{P}$ and P in an A-dimensional space. Kimura (1983) indicated that D can be viewed as the percent error of the estimated accumulated age proportion (i.e., the percent error of $\sum p_i = 1$).

This paper derives a new method for the optimum allocation of ALK, applying the properties of Vartot and Cauchy-Schwarz inequality (Kendall and Stuart 1977). The optimum sizes of length sample and age subsample are determined so that either Vartot is minimized subject to a fixed total cost or the total cost is minimized subject to a desired level of Vartot. Although this method is basically derived for the problem that all age classes are of equal interest, it can be modified by adding weighting factors to the ages which are important to population dynamics. This method was applied to Pacific cod, *Gadus macrocephalus*, from the Washington coast; sablefish, *Anoplopoma fimbria*, from the Gulf of Alaska; and walleye pollock, *Theragra chalcogramma*, from the eastern Bering Sea.

METHODS

Two subsampling schemes related to ALK are frequently used by fisheries biologists: 1) fixed age sub-

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sampling, in which the size of age subsample in all length strata is constant (i.e., $n_j = n/L$, where $n = \sum n_j$ is total age subsample size), and 2) random age subsampling, in which the size of the age subsample in each length stratum is proportional to the length sample size for all length strata (i.e., $n_j = nl_j$). Thus applying Equations (2) and (3), Vartot for a fixed age subsample (Appendix A) is

$$\text{Vartot} = \frac{a_1}{n} + \frac{a_2}{N} \tag{4}$$

and Vartot of a random age subsample is

$$\text{Vartot} = \frac{b_1}{n} + \frac{b_2}{N} \tag{5}$$

where $a_1 = \sum_{i=1}^{A} \sum_{j=1}^{L} [L\, l_j^2\, q_{ij}\,(1 - q_{ij})]$

$$a_2 = b_2 = \sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_i)^2]$$

$$b_1 = \sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\, q_{ij}\,(1 - q_{ij})].$$

It should be noted that a_1, a_2, b_1, and b_2 are all positive values.

The total cost of a survey can be expressed as some function of the costs of the two sampling stages. The commonly used form of the cost function is a simple linear equation relating the unit cost of observing the length and the age of a fish to N and n (Tanaka 1953; Kutkuhn 1963; Southward 1963):

$$C = c_1 N + c_2 n \tag{6}$$

where C is the total cost, c_1 is the unit cost of observing the length of a fish, and c_2 is the unit cost of determining the age of a fish. For optimum allocation, the problem becomes one of determining the values of N and n, which will provide an estimated age composition with a minimum Vartot subject to a given total cost C.

Cauchy-Schwarz inequality, which is frequently used in sampling theory (Cochran 1977; Kendall and Stuart 1977; Schweigert and Sibert 1983), is applied to find optimum set of N^* and n^* for an ALK. The set of N^* and n^* is obtained when they minimize the product of D^2 (= Vartot) and C.

For a fixed age subsample, using Equations (4) and (6) and the Cauchy-Schwarz inequality (Appendix B), we obtain

$$r^* = (n/N)^* = \sqrt{a_1 c_1 / a_2 c_2}. \tag{7}$$

This quantity is the optimum subsampling ratio (r^*) required to reach the minimum (min.) Vartot subject to the cost function given in Equation (6). Therefore, N^* and n^* are dependent on Equation (6):

$$N^* = C/(c_1 + c_2 r^*) \tag{8}$$

$$n^* = r^* N^* \tag{9}$$

$$\text{min. Vartot} = \frac{a_1}{n^*} + \frac{a_2}{N^*}. \tag{10}$$

Similarly, the optimum allocation of a random age subsample can be obtained using Equations (5) and (6) and the Cauchy-Schwarz inequality. The solutions of r^*, N^*, n^*, and min. Vartot are

$$r^* = (n/N)^* = \sqrt{b_1 c_1 / b_2 c_2} \tag{11}$$

$$N^* = C/(c_1 + c_2 r^*) \tag{12}$$

$$n^* = r^* N^* \tag{13}$$

$$\text{min. Vartot} = \frac{b_1}{n^*} + \frac{b_2}{N^*}. \tag{14}$$

Generally, survey designs are based on two constraints (Schweigert and Sibert 1983). The first, as derived previously, relates to obtaining the precision of p_i, viz., to minimize Vartot at a fixed total cost. The second determines the total cost required to achieve a given precision, that is, to minimize total cost (min. C) at a desired level of Vartot. In the latter problem, r^* in Equations (7) and (11) will also minimize the product of D^2C irrespective of the value of C and D^2, i.e., it will minimize D^2 for fixed C or C for fixed D^2 (Kendall and Stuart 1977, Section 39.20). The solutions of n^* and N^* are now dependent on the desired level of Vartot.

For a fixed age subsample, substituting r^* of Equation (7) into Equation (4), we obtain

$$N^* = (a_1/r^* + a_2)/D^2 \tag{15}$$

$$n^* = r^* N^* \tag{16}$$

$$\text{min. } C = c_1 N^* + c_2 n^* \tag{17}$$

For a random age subsample, N^* is obtained by substituting Equation (11) into Equation (5)

$$N^* = (b_1/r^* + b_2)/D^2 \quad (18)$$

$$n^* = r^*N^* \quad (19)$$

$$\text{min. } C = c_1N^* + c_2n^*. \quad (20)$$

Because $0 < r \leqslant 1$, Equations (7) and (11) indicate that

$c_1/c_2 \leqslant a_2/a_1$ for fixed age subsample and

$c_1/c_2 < b_2/b_1$ for random age subsample

must be held for the optimum allocation. When equality holds, $r = 1$ and then ALK degenerates to a simple random sampling for age samples.

EXAMPLES

Three sets of ALK data are used for the example: Pacific cod, aged by the scale method, from the Washington coast (Kimura 1977); sablefish, aged by the otolith method, from the Gulf of Alaska; and walleye pollock, aged by the otolith method, from the eastern Bering Sea (Lai 1985). The parameters of Vartot, a's and b's, are calculated and summarized in Table 1. Accurate cost estimates are difficult to determine; therefore, time measurements required for observing a length and determining an age of fish are used for c_1 and c_2. The total cost C is thus the total time required to build an ALK. The measurements of c_1 and c_2 for the three species (Table 1) are primarily based on the author's experience.

Given a total of 120 working days and 6 working hours per day to a fisheries scientist, the optimum allocation is summarized in Table 2. Under this budget, a random age subsample can provide higher precision than a fixed age subsample (improved 10%, 15%, and 18% respectively for Pacific cod, sablefish, and walleye pollock). Also, for this budget, the error of estimated cumulated age proportion is less than 2.5% for the three species using either fixed or random age subsamples.

Using Equations (7), (15), (16), and (17) for a fixed age subsample and Equations (11), (18), (19), and (20) for a random age subsample, costs under various desired D are minimized for the three species (Table 3). At the same level of D, a fixed age subsample requires much larger sample sizes of length and age than a random age subsample does for the three species. The greatest benefit of using random age subsample is that it drastically reduces the total cost required to obtain the same level of D. The total cost is reduced by 35%, 45%, and 55% respectively for Pacific cod, sablefish, and walleye pollock for any given D when a random instead of a fixed age subsample is used.

Figure 1 shows the relationships of D and total cost. Whether a fixed or a random age subsample is used for the three species, it is obvious that D decreases rapidly until C = 10,000 minutes, which is nearly 70 working days. A point of diminishing

TABLE 1.—Parameters of Vartot and costs for optimum allocation.

	Pacific cod	Sablefish	Walleye pollock
a_1	0.4495	1.2222	1.5501
a_2	0.2660	0.1717	0.1217
b_1	0.2766	0.6235	0.6634
b_2	0.2660	0.1717	0.1217
[1]C	43,200	43,200	43,200
[1]c_1	0.5	0.5	0.5
[1]c_2	15	15	15

[1]In minutes, assuming 120 working days for each species and 6 working hours per day.

TABLE 2.—Optimum allocation of minimizing Vartot for Pacific cod, sablefish and walleye pollock. ($D = \sqrt{\text{Vartot}}$.)

	Pacific cod		Sablefish		Walleye pollock	
	fixed	random	fixed	random	fixed	random
N^*	10,641	13,121	5,534	7,555	5,093	7,551
n^*	2,525	2,443	2,695	2,629	4,064	3,943
D^*	0.014	0.013	0.022	0.019	0.020	0.017

TABLE 3.—Optimum allocation minimizing total cost for various desired precision level ($D = \sqrt{\text{Vartot}}$). Parameters and c_1 and c_2 are listed in Table 1.

		Pacific cod		Sablefish		Walleye pollock	
D		fixed	random	fixed	random	fixed	random
0.05	N^*	865	701	1,073	786	826	557
	n^*	206	130	523	273	659	291
	C^*	3,508	2,307	8,372	4,492	7,002	3,186
0.04	N^*	1,351	1,095	1,676	1,228	1,290	870
	n^*	321	204	817	427	1,030	454
	C^*	5,482	3,605	13,080	7,019	11,940	4,978
0.03	N^*	2,401	1,947	2,979	2,182	2,310	1,547
	n^*	570	362	1,451	759	1,831	808
	C^*	9,745	6,410	23,254	12,478	19,450	8,850
0.02	N^*	5,401	4,380	6,702	4,910	5,160	3,480
	n^*	1,282	815	3,265	1,708	4,118	1,817
	C^*	21,924	14,422	52,320	28,076	43,761	19,912
0.01	N^*	21,604	17,520	26,809	19,640	20,640	13,922
	n^*	5,121	3,262	13,059	6,832	16,473	7,269
	C^*	87,699	57,687	209,279	112,305	175,043	79,650

C^*: in minutes.

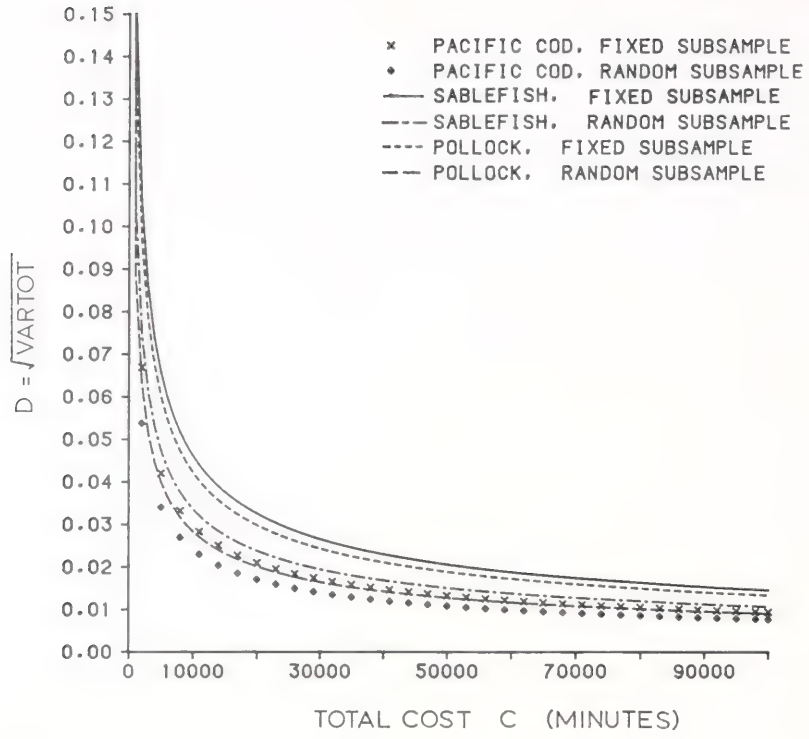

FIGURE 1.—The relationship of D ($= \sqrt{\text{Vartot}}$) and total cost for Pacific cod, sablefish, and walleye pollock, using fixed or random age subsample.

returns is reached beyond this total cost and the curves become flatter for C greater than 10,000. These results indicate that setting a precision at D = 0.02, 0.025, and 0.03 respectively for Pacific cod, walleye pollock, and sablefish using random age subsamples would represent a reasonable compromise between cost and precision. Increasing total cost beyond this level will show no more gains from the ALK.

DISCUSSION

It is obvious that the random subsampling scheme is superior to the fixed subsampling scheme. However, it is more important to realize that there is a cap on total cost for ALK. This cap represents the most effective budget for ALK. Vartot of estimated age composition will not decrease significantly for a greater budget. For the three species, total cost of 10,000 minutes (about 70 working days) is the upper limit. This indicates that approximately 2,000 length observations and 800 random age subsamples for sablefish, 2,500 and 1,200 for walleye pollock, and 3,000 and 600 for Pacific cod represent the best compromise between cost and precision of estimates ($\sqrt{\text{Vartot}}$ = 0.03, 0.025, and 0.02 for the three species respectively).

Although it can be argued that minimizing Vartot may not be sufficient for optimum sampling design for all age classes, it is necessary to consider that some age classes are rare in the commercial catch and are therefore difficult to sample precisely. However, these age classes do not generally represent significant contributions to biomass, and it therefore seems reasonable to concentrate on the major age classes. If these rare age classes are important to population dynamics, the optimum allocation can be addressed as a multiple minima. The objective function can be rewritten as

$$M(N,n) = \sum w_i \, \text{Var}(p_i), \qquad \text{for } i = 1, 2, \ldots, A$$

where w_i is weighting factor. A larger w_i must be given to those age classes which are of interest, whereas the mathematical expressions of optimum allocation are the same as Equations (7) to (14), and subject to the same cost function (Equation (6)), ex-

cept that a's and b's are weighted by w_i. In fact, minimizing Vartot is a special case of minimizing $M(N,n)$ = Vartot for all $w_i = 1$.

Another argument may relate to the possibility that the cost function may be more complicated so that traveling and overhead costs can be taken into account. In such cases, cost function may become a nonlinear form, and the explicit expressions of n^* and N^* cannot be obtained. However, the technique of nonlinear programming can be applied to find numerical solutions of n^* and N^*. In general, it is to

$$\text{minimize} \quad M(N,n) = \sum w_i \, \text{Var}(p_i)$$

$$\text{subject to} \quad C = c(N,n)$$

where C is total cost and $c(N,n)$ is cost function. Many optimization programs can be employed from popular computer software packages for main frame computers. Bunday (1984) provided several BASIC programs for constrained optimization, which may be useful in personal computers. It should be noted, however, that the sufficient and necessary conditions of this constrained minimum must be proved. Theoretically, there is a unique minimum if objective function is convex and constraint function is concave (Bunday 1984).

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APPENDIX A. Derivation of Vartot

For a fixed age subsampling, substituting $n_j = n/L$ into Equation (2), the $\mathrm{Var}(p_i)$ is

$$\mathrm{Var}(p_i) = \sum_{j=1}^{L} \left[\frac{L\, l_j^2\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]. \qquad \text{(A.1)}$$

Applying Equation (3),

$$\mathrm{Vartot} = \sum_{i=1}^{A} \mathrm{Var}(p_i)$$

$$= \sum_{i=1}^{A} \sum_{j=1}^{L} \left[\frac{L\, l_j^2\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]$$

$$= \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [L\, l_j^2\, q_{ij}\,(1 - q_{ij})]}{n} + \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_{ij})^2]}{N}$$

$$= \frac{a_1}{n} + \frac{a_2}{N}$$

which is Equation (4).

For a random age subsampling, substituting $n_j = n\, l_j$ into Equation (2) and applying Equation (3), the Vartot is

$$\mathrm{Vartot} = \sum_{i=1}^{A} \sum_{j=1}^{L} \left[\frac{l_j\, q_{ij}\,(1 - q_{ij})}{n} + \frac{l_j\,(q_{ij} - p_i)^2}{N} \right]$$

$$= \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\, q_{ij}\,(1 - q_{ij})]}{n} + \frac{\sum_{i=1}^{A} \sum_{j=1}^{L} [l_j\,(q_{ij} - p_i)^2]}{N}$$

$$= \frac{b_1}{n} + \frac{b_2}{N}$$

which is Equation (5).

APPENDIX B. Derivation of Equation (7)

The Cauchy-Schwarz inequality (Cochran 1977, p. 97) is

$$(\sum_h A_h^2)(\sum_h B_h^2) - (\sum_h A_h B_h)^2 = \sum_i \sum_{i>j} (A_i B_j - A_j B_i)^2 \geq 0. \quad \text{(B.1)}$$

Therefore,

$$(\sum_h A_h^2)(\sum_h B_h^2) \geq (\sum_h A_h B_h)^2.$$

For a fixed age subsample, let

$$A_1 = \sqrt{a_1/n};\ A_2 = \sqrt{a_2/N};\ B_1 = \sqrt{c_2 n};\ \text{and}\ B_2 = \sqrt{c_1 N}.$$

Applying Equation (B.1), the product of D^2 and C is

$$D^2 C = \left(\frac{a_1}{n} + \frac{a_2}{N}\right)(c_2 n + c_1 N) \geq \left(\sqrt{a_1 c_2} + \sqrt{a_2 c_1}\right)^2. \quad \text{(B.2)}$$

The product D^2C will be minimized, provided that the equality of Equation (B.2) holds. Setting equality of Equation (B.2) and expanding both sides, we find the solution is

$$r^* = (n/N)^* = \sqrt{a_1 c_1 / a_2 c_2} \quad \text{(B.3)}$$

which is Equation (7).

For a random age subsample, let

$$A_1 = \sqrt{b_1/n};\ A_2 = \sqrt{b_2/N};\ B_1 = \sqrt{c_2 n};\ \text{and}\ B_2 = \sqrt{c_1 N}.$$

The reader can derive Equation (11) by the procedures identical to Equations (B.2) and (B.3).

OOCYTE GROWTH AND DEVELOPMENT IN THE STRIPED MULLET, *MUGIL CEPHALUS*, DURING SEASONAL OVARIAN RECRUDESCENCE: RELATIONSHIP TO FECUNDITY AND SIZE AT MATURITY

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ABSTRACT

Oocyte growth and development in the striped mullet, *Mugil cephalus*, were examined during the period of rapid ovarian recrudescence that precedes spawning in coastal waters of northeast Florida. Based on the de novo appearance of yolk proteins detected by polyacrylamide gel electrophoresis, the oocyte size corresponding to the onset of vitellogenic growth was determined to be 0.18 mm (diameter). Through in vitro studies of oocyte responsiveness to steroid stimulation of meiotic maturation, the minimum prematuration oocyte size was determined to be 0.60 mm; largest prematuration oocytes collected during the study were 0.72 mm. Females with vitellogenic oocytes were first collected in Matanzas Inlet in late September. Females with prematurational oocytes were first observed in mid-October. Minimum size at sexual maturity for female striped mullet in northeast Florida ranged from 23 to 27 cm SL.

Oocyte size-frequency profiles led to the development of a staging system for striped mullet ovaries that can be related to simpler measurements of reproductive condition such as the gonadosomatic index and the largest oocyte diameter. According to this system, females with prespawning ovaries first appeared in Matanzas Inlet during mid-October, then disappeared from the Inlet in either mid-December (1985-86 season) or mid-January (1984-85 season). Females with ovaries in spawning condition were not observed in the Inlet during the 2 years of this study, supporting the commonly held assumption of offshore spawning. A few females with postspawn ovaries were collected as early as late November.

The potential fecundity of the striped mullet in northeast Florida was calculated from the size of the single clutch of developing oocytes, and related to both body weight and standard length.

The striped mullet, *Mugil cephalus*, is a euryhaline teleost with a nearly worldwide distribution in marine and estuarine waters. Economically important as a food and bait fish in many areas, the world commercial catch of mullet from 1979 to 1983 averaged nearly 185,000 t (metric tons) per year (FAO 1984). During this time, a yearly average of almost 14,000 t (nearly 8% of the world catch) were caught in the United States, more than in any other single country. Most were caught in the state of Florida, for an average of almost 12,000 t yearly in 1981 and 1982 (National Marine Fisheries Service preliminary data, in Comp and Seaman 1985), equivalent to 87% of the United States and 6% of the worldwide catch. In addition to being the basis of large natural fisheries, *M. cephalus* has been reared for aquacultural purposes in brackish and freshwater ponds (Bromhall 1954; Thomson 1966; Pien and Liao 1975) and has been the subject of induced breeding in the laboratory (Kuo et al. 1973, 1974a, b; Kuo 1982). General information on the biology of *M. cephalus* and related species of mullet can be found in Anderson (1958), Stenger (1959), and Thomson (1966).

Striped mullet have one breeding cycle per year lasting from 2 to 5 months depending on the location (Jacot 1920; Breder 1940; Bromhall 1954; Anderson 1958; Arnold and Thompson 1958; Stenger 1959; Tang 1964; Zhitenev et al. 1974; Pien and Liao 1975; Timoshek and Shilenkova 1975; Finucane et al. 1978; Apekin and Vilenskaya 1979; Azoury and Eckstein 1980; Chubb et al. 1981; Dindo and MacGregor 1981). In coastal waters of the southeast United States, spawning has been reported to occur from October through February as determined from the time of appearance and size of larvae and fry (Anderson 1958; Arnold and Thompson 1958), from the presence of migrating mullet with "developing" ovaries (Breder 1940; Arnold and Thompson 1958; Stenger 1959), and by monthly gonadosomatic index (GSI) changes (Dindo and MacGregor 1981).

In view of the extensive interest in the mullet, it

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is somewhat surprising that so little information concerning its reproduction, other than the seasonal spawning time, is available. For instance, little attention has been paid to the dynamics of oocyte development and ovarian recrudescence in natural striped mullet populations. A staging system for the ovary itself that would simply and meaningfully represent the extent of ovarian recrudescence in this species is lacking. And, although there have been numerous references to size of age at sexual maturity (Jacot 1920; Stenger 1959; Timoshek 1973; Apekin and Vilenskaya 1979), these are generally not based on comprehensive sampling. Similarly, although there have been equally numerous reports of striped mullet fecundity (Nash et al. 1973; Pien and Liao 1975; review by Alvarez-Lajonchere 1982), most derive from counts of eggs (or oocytes) in only a very limited number of fish, while body size-related data are virtually nonexistent.

We recently initiated several studies dealing with the reproduction of *M. cephalus* in coastal waters of northeast Florida and related topics. The specific purposes of this investigation include describing the patterns of oocyte growth during seasonal ovarian recrudescence, developing an ovarian staging system based on these patterns, and providing definitive determinations of both the size at maturity and the size-specific fecundity of female striped mullet in the area.

MATERIALS AND METHODS

Fish

Female striped mullet approximately 18 cm standard length (SL) or larger were captured by cast net from the Matanzas River Inlet south of St. Augustine, FL. Collections were made periodically from October 1984 through January 1985, and again from August 1985 through January 1986, for a total sample of 340 fish. Standard length and fork length (FL) were determined to the nearest 0.1 cm, and body weight (BW) to the nearest 0.1 g for all fish. Ovaries of most (248) fish ≥20 cm SL were removed and transferred to a buffered salt solution (FO: Wallace and Selman 1978), and any adhering non-ovarian tissue was removed. Whole ovaries were then patted dry and weighed to the nearest 0.01 g. The GSI for each fish was calculated as GSI = (ovary weight/body weight) × 100.

Oocyte Size-Frequency Profiles

Oocyte size-frequency profiles were constructed for each fish in the following manner. A representative (see below) piece was gently teased free from the middle of each newly collected ovary, patted dry, weighed to the nearest 0.1 mg, and placed in a petri dish containing FO solution. Pieces weighed from 1 to 9 mg and contained from 100 to 500 oocytes >0.10 mm in diameter. Individual follicle-enclosed oocytes were manually measured to the nearest 0.02 mm with an optical micrometer mounted on a dissecting microscope. Oocyte size-frequency profiles were not determined for fish with largest oocyte diameters (LODs) <0.10 mm, although their LODs were noted.

Profiles and LODs derived from a sample of ovary can be considered representative because oocyte development is known to occur uniformly throughout the mullet ovary (Ochiai and Umeda 1969; Shehadeh et al. 1973; Timoshek and Shilenkova 1975).

Oocyte Stages

The oocyte size at which vitellogenesis (the period of protein yolk accumulation) begins in the striped mullet was determined by the appearance of specific yolk protein bands in oocyte homogenates subjected to polyacrylamide gel electrophoresis (see Greeley et al. 1986b). Groups of small oocytes with mean diameters of 0.14, 0.16, 0.18, and 0.20 mm were isolated from surrounding ovarian tissue, homogenized in a sodium dodecyl sulfate (SDS) containing buffer solution, and heated at 100°C for 5 minutes. Samples were loaded onto a 0.75 mm thick polyacrylamide gradient gel (gradient: 3.5-20.4%) and were electrophoresed in SDS buffer with a constant applied current of 30 mAmps until the bromophenol blue marker migrated from the gel. Protein fixation, visualization with Coomassie blue, and molecular weight determinations were conducted as in Wallace and Selman (1985). Biochemicals and reagents were highest available grades from Sigma Chemical Company[3] and Bio-Rad Laboratories.

The minimum oocyte size competent to resume meiotic maturation (leading to the development of a mature fertilizable egg) in response to steroid hormone stimulation was determined in vitro by the methods of Greeley et al. (1986a). Larger follicle-enclosed oocytes were isolated in FO and assigned to one of four pools with mean diameters of 0.52, 0.56, 0.60, and 0.64 mm. Oocytes from each pool were randomly subdivided into treatment (steroid

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

added) and control groups, and then transferred into separate 35 × 10 mm petri dishes containing 3 mL of a 75% L-15 culture medium (Sigma) at pH 7.5. A solution containing 3 μg of 17α-hydroxy-20β-dihydroprogesterone in 10 μL of 95% ethanol was added to each treatment dish (for a final steroid concentration of 1 μg/mL); 10 μL of 95% ethanol was added to each control dish. Oocytes were incubated at 20°C for 48 hours and then examined for germinal vesicle breakdown (GVBD), which was easily noted by the absence of the germinal vesicle (GV) or nucleus in the highly transparent postmaturation oocyte, as an indicator of the resumption of meiotic maturation in response to the hormone.

Fecundity

Potential fecundity was estimated for each fish whose oocyte size-frequency profile demonstrated that recruitment of oocytes into vitellogenesis had ceased as potential fecundity = [(number of recruited oocytes in ovary piece) × (weight of whole ovary)]/(piece weight).

RESULTS

Gonadosomatic Index (GSI)

Ovarian recrudescence in the striped mullet occurs during autumn and early winter in coastal waters of northeast Florida, as indicated by seasonal changes in the GSIs of females collected from the Matanzas River Inlet (hereafter referred as Inlet) during the 1984-85 and 1985-86 breeding seasons (Fig. 1). In August of 1985, the earliest month of collections for this study, GSIs were <1 in all sampled fish. Ovaries represented by these low GSIs were quite small and were either translucent and colorless (smallest and least developed ovaries) or opaque with a red hue resulting from extensive vascularization (slightly larger and more developed ovaries). Similar low GSIs continued to be found in all females collected through mid-September.

In late September the GSIs of a portion of the collected females rose sharply, to nearly 9. The much larger ovaries represented by these high GSIs were

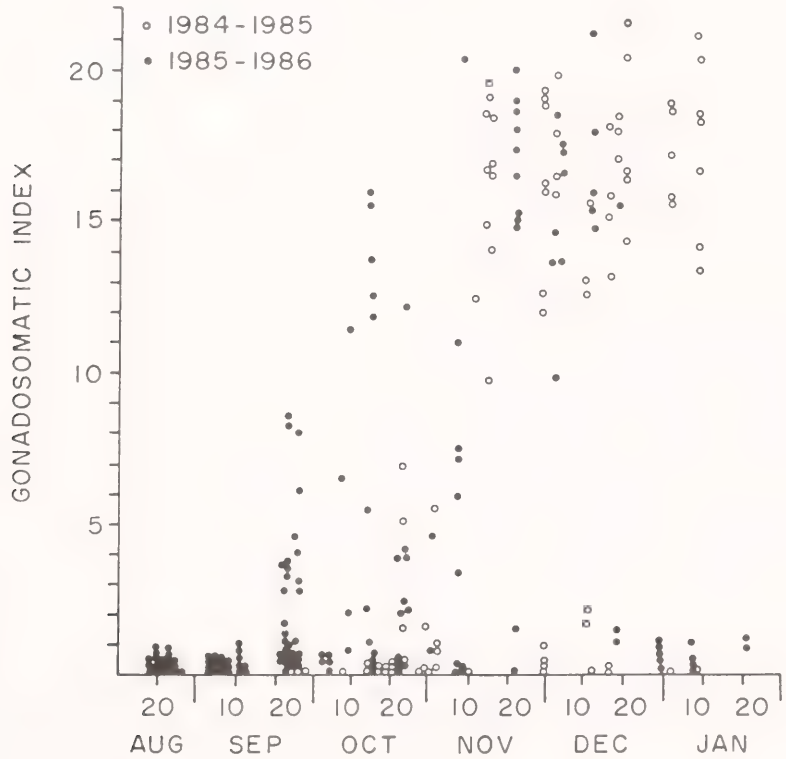

FIGURE 1.—Variation in the gonadosomatic index (GSI) of female *Mugil cephalus* ≥20 cm SL during prespawning ovarian recrudescence along the northeast Florida coast.

now yellow to golden in color because of a preponderance of yellow yolky oocytes in the ovarian lamellae. This initial phase of GSI increases continued through early November, at which time two distinct groupings of females within the population became apparent: those with GSIs remaining <2, and those with GSIs ranging between 10 and 21. Average GSIs in the latter group rose only slightly thereafter, ranging from 13 to 22 by early December. The lower GSIs of the rest of the population remained unchanged throughout the remainder of this study.

During the 1984-85 season, females with high GSIs continued to be caught until mid-January, at which time larger females (≥20 cm SL) apparently left the Inlet because none were caught during the 3 additional weeks of intensive collecting. In contrast, during the 1985-86 season, females with high GSIs were only collected through mid-December. Although a few mid-size females were collected through late January of this year after the expenditure of considerable collecting time and effort, all proved to have small GSIs.

Oocyte Stages

A primary purpose of this project was to document the oocyte growth and development that accompanied these GSI changes during prespawning ovarian recrudescence. Two oocyte development stages of primary interest to us were 1) the stage at which yolk accumulation or vitellogenesis begins, and 2) the stage during, or following, vitellogenic growth when the oocyte first becomes competent to resume meiotic maturation and thereby develop into a fertilizable egg.

We previously showed two large proteins at M_r = 104,000 and 90,000 to be the major yolk proteins present in mullet oocytes at the end of vitellogenic growth (Greeley et al. 1986b). As evidenced by the de novo appearance of these marker proteins (Fig. 2), vitellogenesis in the striped mullet begins in oocytes that are between 0.16 and 0.18 mm in diameter. In this study, oocytes 0.16 mm in diameter and smaller are thus considered to be previtellogenic, a broad classification including both primary growth- and yolk vesicle-stage oocytes as described

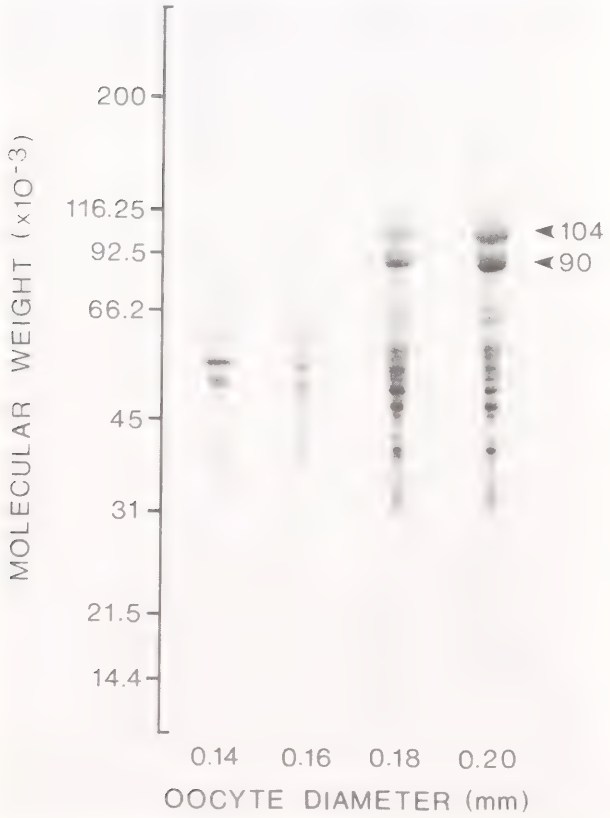

FIGURE 2.—Polyacrylamide gel electrophoresis of oocyte proteins indicating de novo appearance of yolk proteins in vitellogenic oocytes (0.18 mm in diameter) of the *Mugil cephalus*, with comparison to smaller previtellogenic and larger vitellogenic oocytes (see text). Molecular weight standards are indicated on the left for comparison; the molecular weights of the two major yolk proteins are shown on the right (arrows).

by Wallace and Selman (1981); oocytes 0.18 mm in diameter and larger are considered to be actively vitellogenic.

Late vitellogenic oocytes become competent to resume meiotic maturation and develop into a fertilizable egg in response to an in vitro steroid challenge at 0.60 mm in diameter, with larger oocytes being only marginally more responsive (Table 1). Therefore, oocytes 0.60 mm and larger that do not exhibit any signs of maturation such as yolk "clearing" or hydration are considered to be in a prematuration stage of development.

Striped mullet eggs following meiotic maturation are even larger (0.90 to 1.00 mm in diameter) (Abraham et al. 1966; Nash et al. 1973; Pien and Liao 1975; Finucane et al. 1978; Greeley et al. 1986b), nearly transparent (yolk has cleared), hydrated, float in full-strength seawater, and thus are easily distinguished from the smaller and more opaque prematuration oocytes. Females with mature eggs were not collected during this study.

TABLE 1.—Percentage of different-sized striped mullet oocytes undergoing germinal vesicle breakdown (GVBD) in vitro in response to treatment with 17α-hydroxy-20β-dihydroprogesterone (1 μg/mL) or an ethanol control.

Oocyte diameter (mm)	Treatment	*N*	(%)GVBD
0.52	control	55	0
	steroid	50	0
0.56	control	50	0
	steroid	45	0
0.60	control	326	0
	steroid	301	65
0.64	control	196	0
	steroid	198	71

Largest Oocyte Diameter (LOD)

The relationship of oocyte diameter to stages of oocyte development is clearly delineated in Figure 3. Three major developmental stages are shown: 1) previtellogenic growth, including both the pri-

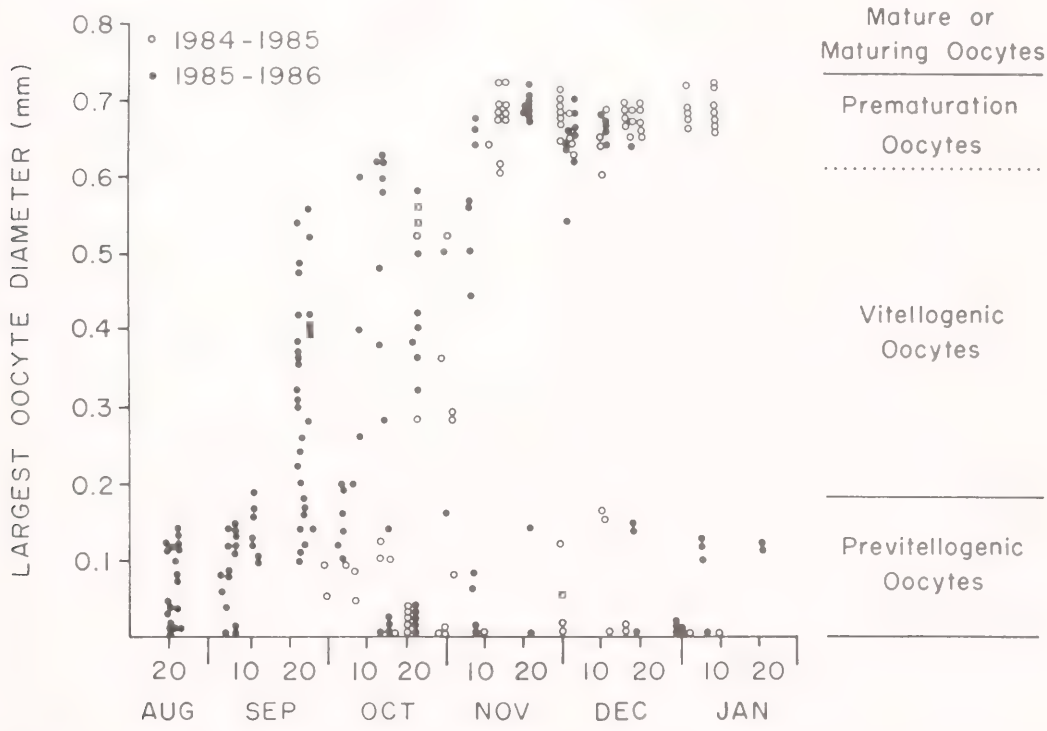

FIGURE 3.—Variation in the largest oocyte diameter (LOD) of female *Mugil cephalus* ≥20 cm SL during prespawning ovarian recrudescence along the northeast Florida coast. Presented on the right are oocyte developmental stages corresponding to these oocyte sizes. Broken line between vitellogenic and prematuration designations signifies uncertainty concerning whether the latter is actually a substage of the former. The category "previtellogenic" encompasses both primary growth and yolk vesicle oocytes.

mary growth and yolk vesicle phases as defined by Wallace and Selman (1981), 2) vitellogenic growth, and 3) maturation. An additional developmental category—prematuration—may or may not be considered a substage of late vitellogenesis; although oocyte growth appears to level off at this time, we have no direct evidence that the oocyte completely ceases to take up yolk precursors at this time.

Changes in the LOD (Fig. 3) during the period of seasonal ovarian recrudescence were similar to changes in the GSI. LODs were small in August and early September, representative of still previtellogenic oocytes. LODs then rose sharply in mid-September as vitellogenic oocytes began to appear in females captured in the Inlet. The range of LODs in the population at this time varied considerably, from <0.01 mm in some fish to nearly 0.56 mm in others. LODs continued to rise in one portion of the population through mid-November, before leveling off between 0.60 and 0.72 mm; in other females, LODs remained below 0.18 mm through the end of each study period. Females with high LODs were last collected in mid-December during the 1985-86 breeding season and in mid-January during the 1984-85 season.

Body Size at Maturity

An examination of the LODs as a function of standard length on a month to month basis (Fig. 4) reveals several body size-related trends that bear on the results presented in Figure 3. During August, the first month of the collections, there was little difference between the LODs of different-sized females, all being low and representative of previtellogenic oocytes. Only a few large striped mullet were collected during this month. This changed in September, with larger females over 32 cm SL becoming more prevalent in the Inlet and exhibiting a tendency to have higher LODs than smaller females. By October, smaller females (to a lower limit of 28 cm SL) also began to acquire vitellogenic oocytes, although their average LODs were still lower than those of larger females. During November, LODs of larger females leveled off at 0.60 to 0.72 mm, but a few smaller females (now to a lower limit of 26 cm SL) continued to have intermediate LODs indicative of oocytes in the early stages of vitellogenesis. By December and January, recruitment of smaller females into sexual maturity apparently ceased because LODs were now uniform—either greater than the 0.60 mm prematurational oocyte size or less than the minimum 0.18 mm vitellogenic size—in all females regardless of body size.

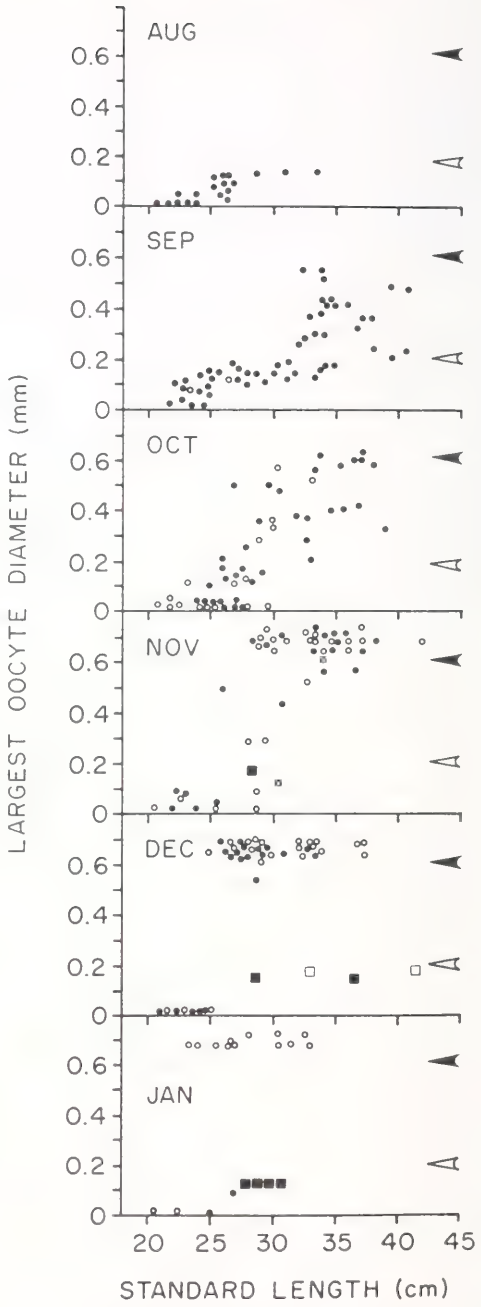

FIGURE 4.—Monthly variation in the relationship of the largest oocyte diameter (LOD) to standard length (SL) in female *Mugil cephalus* during prespawning ovarian recrudescence along the northeast Florida coast. Circles represent data points from prespawning females (open: 1984-85; closed 1985-86); squares represent data points from postspawn females (open: 1984-85; closed 1985-86). Open arrows indicate oocyte size at beginning of vitellogenesis; solid arrows indicate minimum prematuration oocyte size.

During November, December, and January, a few larger females with LODs less than the minimum 0.18 mm vitellogenic size were collected from the Inlet. This suggested that seasonal ovarian recrudescence does not occur in all large females every year. However, other criteria (see below) indicated that these were actually postspawn ovaries.

Minimum female size at maturity by the end of the season ranged from 23 to nearly 27 cm SL. Three size-categories of females can now be recognized: 1) those smaller than 23 cm SL that are obligatory immatures; 2) those 23 to 27 cm SL that may enter into maturity before the end of the spawning season; and 3) those larger than 27 cm SL that are always sexually mature sometime during the spawning season. The minimum body size at sexual maturity can also be expressed as a function of fork length (27 to 31 cm) or body weight (232 to 383 g) with the use of the equations provided in Figure 5.

Ovary Stages

LODs are useful criteria for following the course of ovarian recrudescence in the striped mullet and for determining the size or age of females at sexual maturity. Yet the LOD by itself cannot distinguish between sexually immature and postspawn females,

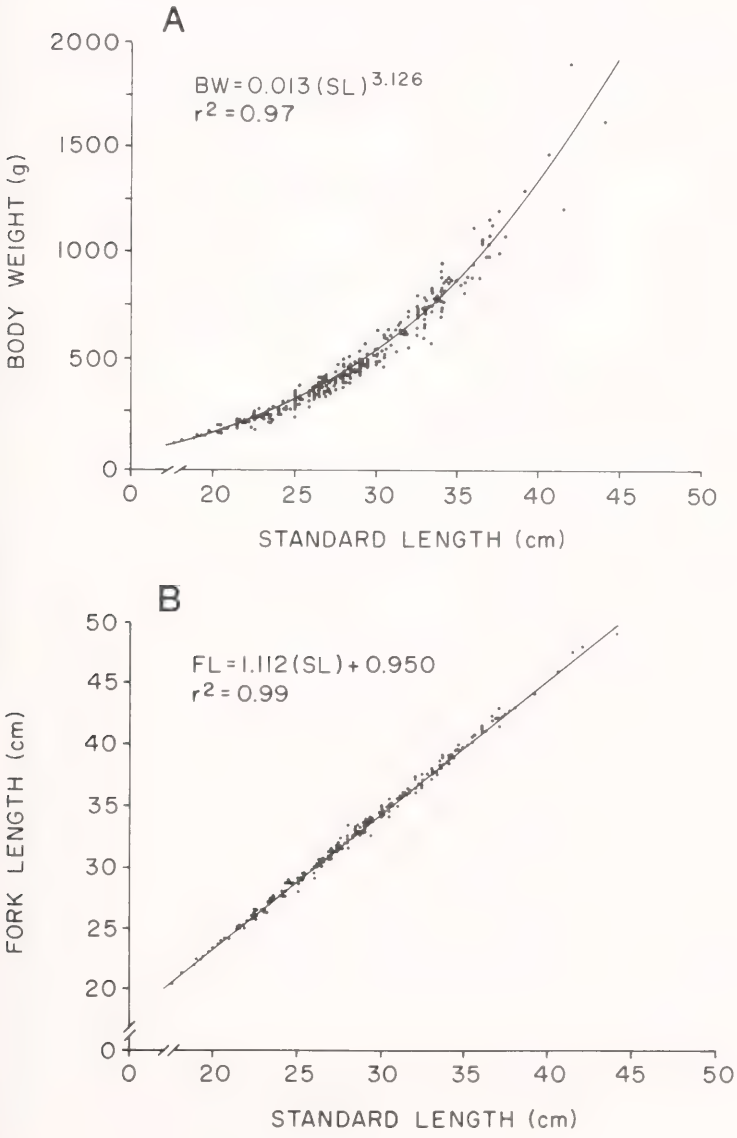

FIGURE 5.—Relationship of (A) body weight and (B) fork length to the standard length of female *Mugil cephalus* (≥20 cm SL) during prespawning ovarian recrudescence along the northeast Florida coast. Lines were fitted by least squares regression.

nor does it provide information about the range of oocyte sizes to be found in individuals. To better understand the pattern of oocyte development leading to the formation of a clutch of mature eggs, it is necessary to examine comprehensive oocyte size-frequency profiles. Representative profiles of Figure 6 illustrate both the pattern of oocyte development during ovarian recrudescence in the striped mullet and an ovarian staging system based upon these profiles.

In ovarian stage I (previtellogenesis), yolk accumulation by developing oocytes has not yet begun, as all oocytes are less than the minimum previtellogenic size of 0.18 mm in diameter. An oocyte size-

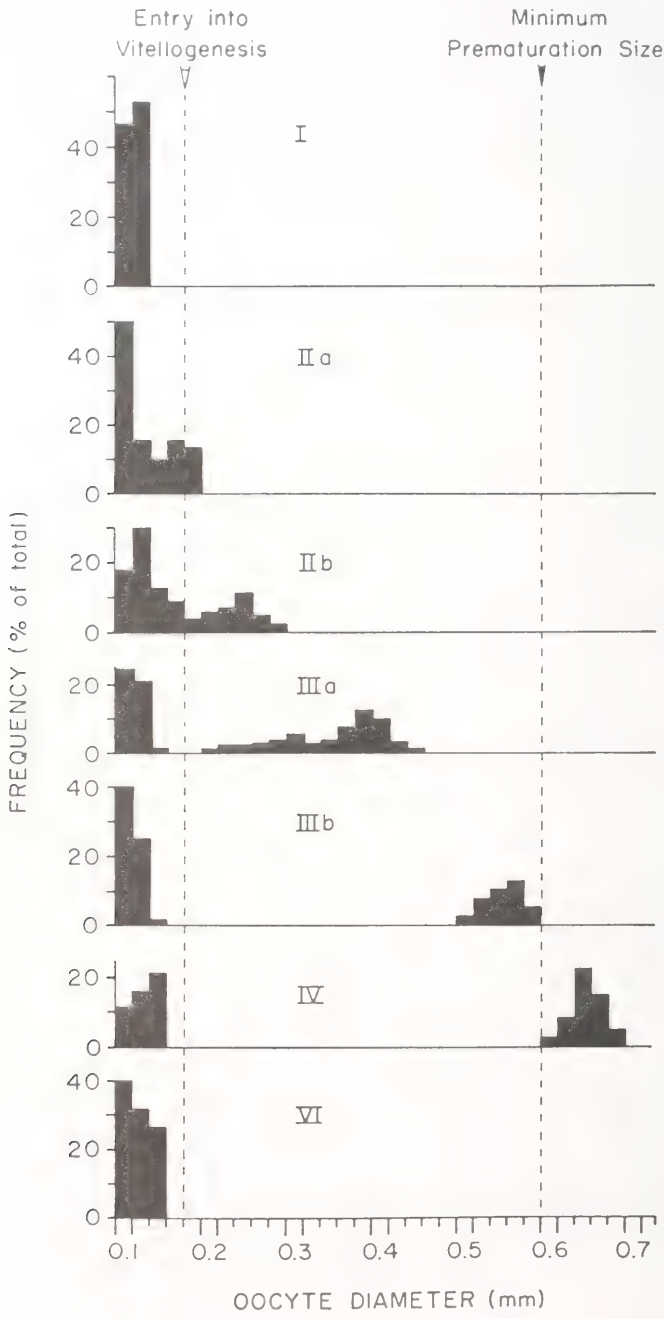

FIGURE 6.—Representative oocyte size-frequency profiles corresponding to stages of ovarian recrudescence in *Mugil cephalus*. Dashed line on left represents the transition between previtellogenic and vitellogenic oocytes; dashed line on the right delineates the minimum prematuration oocyte size. See text for explanation of stages.

frequency profile from an ovary in this stage is shown in Figure 6. GSIs of females with stage I ovaries ranged up to 0.8.

Stage II (early vitellogenesis) is characterized by recruitment of previtellogenic oocytes into vitellogenesis. A single clutch of vitellogenic oocytes starts to form, becoming distinct from the remaining mass of previtellogenic oocytes as the recruited oocytes increase in diameter due to yolk accumulation. This stage can be further divided into two substages on the basis of the appearance of the profiles. In stage IIa, recruitment into vitellogenesis has just begun; a clear separation between the developing (vitellogenic) and nondeveloping (previtellogenic) oocytes is not yet discernible. In stage IIb, the developing clutch forms a distinct peak (or peaks) as recruitment and subsequent vitellogenic growth continues. LODs of females with stage II ranged from 0.18 to 0.56 mm; GSIs varied from 0.3 to 8.5.

In stage III (mid- to late-vitellogenesis), recruitment into vitellogenesis ceases, although oocytes in the recruited clutch continue to increase in diameter due to further yolk accumulation. This stage can also be divided into two substages. In stage IIIa, recruitment has just ended: the recruited clutch is spread out in size, and multiple size-frequency peaks are apparent. In stage IIIb, the recruited clutch tightens into a single peak; oocyte diameters continue to increase. LODs of females with stage III ovaries varied from 0.40 to 0.59 mm; GSIs ranged from 2.1 to 12.1.

In stage IV (prespawning), oocytes in the recruited clutch reach the minimum prematuration size of 0.60 mm in diameter and become capable of resuming maturation in response to a hormonal signal. Late in the stage, as shown in Figure 6, all oocytes in an ovary will be at, or above, the minimum prematuration size. LODs of females with stage IV ovaries were 0.60 and 0.72 mm; GSIs were more scattered, from a low of 11.4 to a high of 21.2.

Stage V (spawning: not shown) is characterized by the presence in the ovary of maturing oocytes or mature eggs. No fish with ovaries in this stage were caught in the Inlet; however, this stage was produced in the laboratory by injection of human chorionic gonadotropin into prespawning females (Greeley et al. 1986b).

Stage VI (postspawn) ovaries, upon gross examination, are small, red, and flaccid in appearance with a thickened ovarian wall. Spawning is apparently complete—at least by the time the females return to the Inlet—as no partially spawned ovaries were collected, nor were large atretic oocytes or eggs ever observed. LODs of postspawn females were 0.12 to 0.14 mm; GSIs ranged from 0.1 to 1.6.

Monthly changes in the relative frequency of these stages in females collected from Matanzas Inlet during ovarian recrudescence in 1985-86 are shown in Figure 7. The variation in these stages is similar to the variation observed in the LOD, although the ovarian stages provide a somewhat different infor-

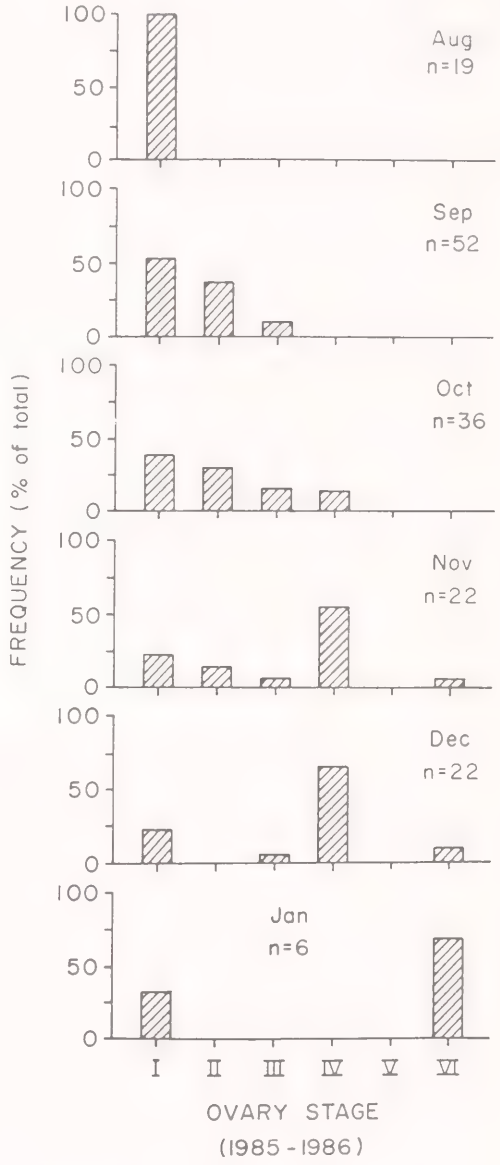

FIGURE 7.—Monthly variation in ovarian stages of adult *Mugil cephalus* (≥20 cm SL) during prespawning ovarian recrudescence along the northeast Florida coast. Data presented for the 1985-86 season only (see text).

mation. In August, only fish with previtellogenic ovaries (stage I) were collected. During September and October, a variety of ovary stages were observed, from previtellogenic (stage I) to prespawning (stage IV). Ovaries with active recruitment of oocytes into vitellogenesis (stages IIa and b) were not observed after October. The first postspawn fish (stage VI) was caught in late November, and by January only previtellogenic or postspawn fish were caught. Variation in ovary stages during the 1984-85 season (not shown) was similar, except that in this year females with prespawning (stage IV) ovaries were collected as late as mid-January.

Fecundity

Because oocyte size-frequency profiles indicate that only a single clutch of developing oocytes proceeds through vitellogenesis in a season, and that this single clutch is eventually spawned in its entirety, it is possible to calculate the individual fecundity of a female striped mullet by counting the number of vitellogenic oocytes in stages IIIa-IV ovaries (in which recruitment of oocytes into developing clutches has ceased). The annual potential fecundity, or number of eggs available to be spawned in a single breeding season, was thus found to be linearly related to body weight and geometrically related to standard length (Fig. 8). The lowest fecundity observed was 0.25×10^6 eggs in a fish 264 g BW and 23.5 cm SL, and the highest fecundity was 2.2×10^6 eggs in a fish 1,627 g BW and 44 cm SL.

DISCUSSION

The present results indirectly confirm that the spawning season of *M. cephalus* in coastal waters of northeast Florida extends from at least late November (when the first postspawn female was collected during the 1985-86 season) through mid-January (when the last prespawn female was collected during the 1984-85 season). However, there is probably a certain amount of year-to-year variation within this range: the first postspawn female was not observed until December during one season (1984-85), while the last prespawn in another (1985-86) was collected in December rather than January.

It is also probable that these dates are in reality only a conservative estimate of the actual range of the striped mullet spawning season in this area. Available evidence from other studies strongly suggest that striped mullet spawn offshore (Anderson 1958; Arnold and Thompson 1958; Finucane et al. 1978). If this is also true of striped mullet in northeast Florida, then postspawn females collected in November may have traveled extensively between spawning at offshore sites and their eventual capture in the Inlet. Likewise, the prespawn females collected in January would have required some time to reach offshore spawning sites after leaving the Inlet. Therefore, adding a month to each end of the observed range to conservatively account for such migrations may be appropriate and would make our dates consistent with previously published reports of spawning times for striped mullet in the southeast United States ranging from October through February (Broadhead 1956; Anderson 1958; Dindo and MacGregor 1981).

Do striped mullet of northeast Florida actually spawn offshore? The best evidence for offshore spawning migrations in this study was our failure to collect from the Inlet any females with spawning ovaries or even partially spent ovaries, suggesting that spawning probably occurred some distance from the Inlet. Further evidence for an offshore spawning site were the abrupt disappearances from the Inlet of fish with prespawning ovaries during both years of the study (mid-January 1984-85 and mid-December 1985-86), as this behavior suggested that mass spawning migrations to offshore waters occurred at these times.

If these disappearances did represent mass offshore spawning migrations, then how can we explain the earlier appearances in the Inlet of a few postspawn fish? Perhaps there are actually multiple spawning migrations, possibly by different populations of striped mullet moving through the Inlet at intervals throughout the period. Or perhaps some inshore spawning also occurs: staff at the Whitney Laboratory[4] have occasionally observed what they considered to be striped mullet spawning activity in the Intracoastal Waterway near the Inlet, and there are a few anecdotal accounts of inshore spawning in the literature (Breder 1940; Gunter 1945; Timoshek and Shilenkova 1975). However, if inshore spawning does occur, it must be limited in scope; otherwise, we would have collected females with spawning ovaries in the Inlet during our own studies. It may be that striped mullet can spawn either inshore or offshore, with offshore spawning favored, depending on factors—such as salinity, temperature, winds, currents, tides, or some combination thereof—which vary from locale to locale and from year to year.

[4]W. Raulerson, Whitney Laboratory, University of Florida, Route 1, Box 121, St. Augustine, FL 32086, pers. commun.

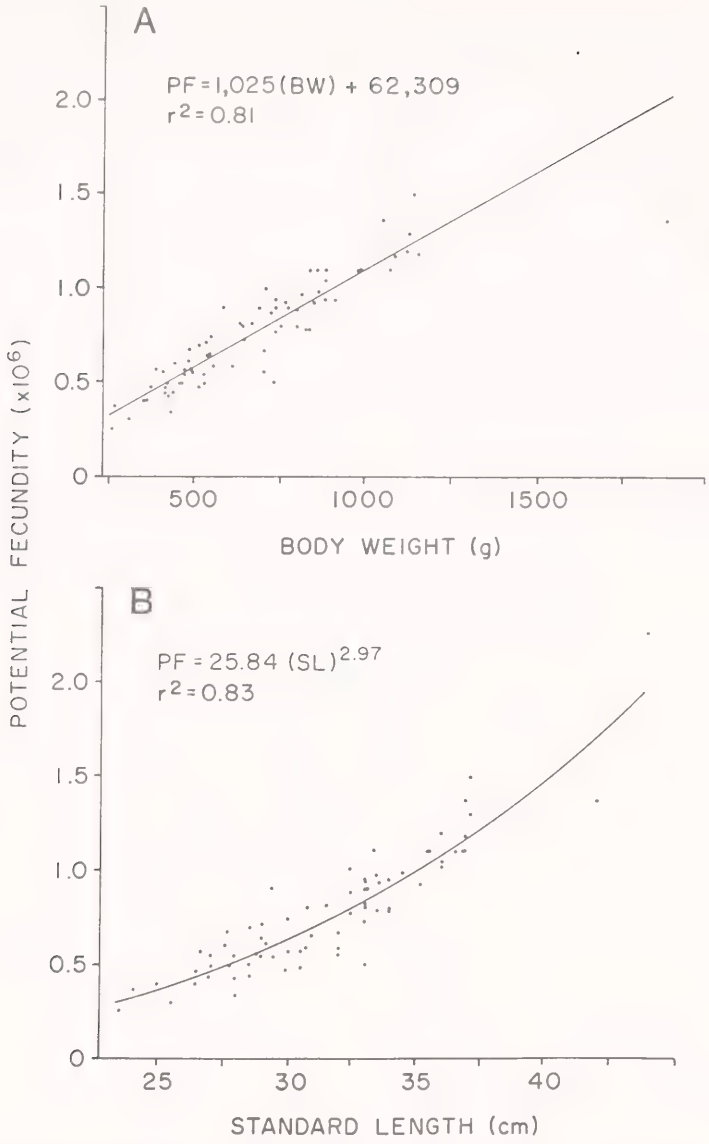

FIGURE 8.—The relationship of the potential annual fecundity of *Mugil cephalus* from northeast Florida to (A) body weight and (B) standard length. Lines are drawn from regression equations.

In fact, the apparent timing of the hypothetical final spawning migrations from the Inlet in each of the two seasons of the present study suggests there might be a tidal involvement in these events: one coincided with a set of new moon spring tides, and the other to a set of full moon spring tides. Such a tidal or lunar connection to spawning migrations of striped mullet has been proposed previously (Bromhall 1954), although supporting evidence is still inconclusive. Others have alternatively suggested wind and currents might be contributing factors to the onset of spawning migrations (Apekin and Vilenskaya 1979); further work is needed to clarify these issues.

Most workers agree that individual female *M. cephalus* spawn only once a year (Zhitenev et al. 1974; Timoshek and Shilenkova 1975; Chubb et al. 1981). Our results support this assumption, as we never observed more than a single clutch of developing oocytes proceeding through vitellogenesis dur-

ing the fall period of prespawning ovarian recrudescence. Our failure to collect any partially spawned females is also consistent with a single seasonal spawn.

In this study, both the GSI and the LOD proved to be adequate, although not completely satisfactory, indicators of the reproductive condition of female striped mullet. However, of these two indices the LOD would appear to be preferable. Determination of the LOD requires only the biopsy of a small piece of ovary (see Shehadeh et al. 1973) which can be easily accomplished without harm to the fish, while determination of the GSI requires the sacrifice of the fish. Furthermore, the validity of the GSI has been questioned (deVlaming et al. 1982) as to its accuracy in correcting for body size in a consistent manner over all reproductive stages.

On the other hand, the speed and ease of obtaining the LOD are its only advantages over a more comprehensive indicator of reproductive condition —the oocyte size-frequency profile. Such a profile also requires only the biopsy of a small piece of ovary and is a much more accurate indicator of ovarian stage, especially during the active vitellogenic growth of the ovary when a developing clutch may be quite spread-out in size.

An adequate understanding of the functional relationship between oocyte size and stage is, of course, required for correct interpretation of either LODs or oocyte size-frequency profiles. Of particular interest to us during this study were the sizes of the oocyte at 1) the beginning of vitellogenesis and 2) the prematuration stage of development. Our data indicate that oocytes of the striped mullet are able to grow to a point immediately prior to vitellogenic growth, then temporarily arrest at that stage. In contrast, once vitellogenic growth begins, further development leading to a subsequent clutch of mature eggs is apparently ensured. Thus knowledge of this transition point is extremely important to investigators attempting to predict the future reproductive status of these fish. Likewise, clearly identifying the prematuration stage of oocyte is important because at this stage the oocyte is competent to resume meiotic maturation culminating in the formation of a fertilizable egg.

We define the beginning of vitellogenesis in the striped mullet oocyte by the initial appearance of yolk proteins detectable by electrophoretic techniques and the prematuration stage of development by in vitro culture techniques. Our resulting prematuration stage is in essential agreement with the "functional maturity" stage of Kuo et al. (1974b), as is our 0.18 mm initial vitellogenic stage with the initial "yolk globule" stage (0.20 mm) of these authors. We did not examine smaller oocytes in detail and thus did not attempt to establish specific stages for previtellogenic oocytes.

The oocyte size-frequency profiles of this study, plus the additional data relating oocyte sizes and stages, demonstrate that *M. cephalus* has a group-synchronous type of oocyte development, as originally defined by Marza (1938) and reiterated by Wallace and Selman (1981). In such an ovary, a single developing clutch of oocytes coexists with an apparently asynchronous pool of previtellogenic oocytes. However, it must be pointed out that in the mullet this pattern is not always straightforward. The movement of oocytes into vitellogenesis is quite prolonged in time, so that a truly discrete clutch, as characterized by the cessation of additional recruitment into the clutch, does not become apparent until the more developed oocytes within the clutch are already well into vitellogenic growth. Furthermore, even after recruitment into vitellogenesis ceases, the developing clutch can be quite heterogenous in size (see oocyte size-frequency profile for ovarian stage IIIa, Figure 6) and thus may not appear to be undergoing synchronous growth until ovarian stage IIIb. Such a pattern of oocyte development could be very difficult to characterize without examination of ovaries from females collected throughout the period of ovarian recrudescence.

To the best of our knowledge, the ovary staging system put forth in this paper is the only such comprehensive system developed specifically for the striped mullet. Based on well-defined and physiologically significant criteria, it is presented with the purpose of standardizing future studies dealing with reproduction in the striped mullet.

The range (23 to 27 cm SL) we present for the size at maturity of striped mullet in northeast Florida is similar to the only other published report for the area (25 cm SL by Stenger 1959), but much lower than the values (30 to 46 cm SL) reported by Jacot (1920), Thomson (1951), Ochiai and Umeda (1969), Timoshek (1973), and Apekin and Vilenskaya (1979). Most investigators agree that female mullet reach sexual maturity at the end of their third year (Thomson 1951; Timoshek 1973). We made no attempt to age the fish because methods available were not always agreed upon (see Thomson 1966). However, according to the growth schedules of Thomson (1966), adapted from various primary sources, the age at maturity in this study apparently ranged from 2¼ years (23 cm SL) to 2½ years (27 cm SL).

It thus appears that female *M. cephalus* attain sex-

ual maturity in northeast Florida at a smaller size, and probably at an earlier age, than anywhere else in the world. However, caution must be taken in making such comparisons. Our results demonstrate that smaller fish typically lag behind larger fish in reaching a sexually developed state by as much as 2 months on a seasonal basis. In consequence, the determinations of size or age at maturity by other investigators, if based on only a limited number of samples or on samples obtained at only a limited number of dates within the prespawning period of ovarian recrudescence, might not be truly comparable to our results.

The annual fecundity of *M. cephalus* has been reported to be from 1.2×10^6 to 2.8×10^6 by most authors (Thomson 1966), although estimates ranged from as low as 0.5×10^6 to as high as 14×10^6 (from review by Alvarez-Lajonchere 1982). Unfortunately, the methods whereby these values were obtained are often not given, so many reports have to be considered suspect. In addition, data concerning size-related trends in the fecundity of striped mullet are nearly nonexistent. By contrast, our estimates of fecundity (0.25×10^6 to 2.5×10^6) are well-documented and demonstrate a clear and highly predictable relationship between individual fecundity and body size.

In conclusion, this study describes the pattern of oocyte development during seasonal ovarian recrudescence in the striped mullet, proposes an ovarian staging system based on oocyte stages and size-frequency profiles, gives a range of values for the female size at maturity, and presents the only comprehensive examination of size-related fecundity for *M. cephalus* to date.

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DEVELOPMENT OF THE EGGS AND LARVAE OF THE YELLOWCHIN SCULPIN, *ICELINUS QUADRISERIATUS* (PISCES: COTTIDAE)

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ABSTRACT

The development of the eggs and larvae of *Icelinus quadriseriatus* is described from laboratory-reared and field-collected specimens.

The eggs have diameters from 1.08 to 1.17 mm, an adhesive chorion, and multiple oil globules. Before hatching the oil globules coalesce into one 0.14-0.19 mm in diameter. The embryo develops a patch of tubercles on the dorsal surface of the head that are lost immediately after hatching.

The larvae hatch at 2.6-3.4 mm. Distinguishing characters are 1-6 rows of ventral gut melanophores, 25-63 postanal ventral melanophores, and lower jaw angle pigment. Larvae over 3.9 mm may develop chin and pectoral insertion melanophores. Nasal and parietal spines appear at 9.3 mm. Postflexion larvae develop three patches of pigment dorsolaterally on the body by 10.5 mm and transform to juveniles by 16.3 mm.

Scorpaeniform fishes are represented in the North Pacific Ocean by a large group of endemic taxa whose early life histories are poorly known. The early life histories of many sculpins (Cottidae), the second largest family in the order, were recently described (Richardson and Washington 1980). Larvae of several species of *Artedius*, *Clinocottus*, and *Oligocottus* have been described by Washington (1986). *Synchirus gilli* larvae were described by Marliave et al. (1985). Reared and field-collected larvae of *Chitonotus pugetensis* have been described (Misitano 1980; Richardson and Washington 1980); however, the larval stages of the closely related *Icelinus*, including nine described species and one undescribed species (Yabe et al. 1980; R. Rosenblatt[2]), are unknown. The purpose of this paper is to describe the eggs and larvae of the yellowchin sculpin, *Icelinus quadriseriatus*, using both laboratory-reared and field-collected material.

Icelinus quadriseriatus occurs along the coast of California north to Sonoma County (lat. 38°23.5′N; long. 123°08′W) and south to Cabo San Lucas, Baja California (Miller and Lea 1972; Eschmeyer et al. 1983). Adults are usually collected at depths from 18 to 90 m (based on Natural History Museum of Los Angeles County (LACM) and California Academy of Sciences (CAS) adult collection data); occasionally they range beyond these limits, being found in the intertidal zone and as deep as 201 m (Love and Lee 1974). The period of peak occurrence of prespawning females for *I. quadriseriatus* ranges from January to April, but mature oocytes have been found in females in every month except October (in one year of a 2-yr study) indicating an almost year-round spawning capability (Goldberg 1980).

MATERIALS AND METHODS

Adult *I. quadriseriatus* were collected by otter trawl off Santa Monica, CA, on 8 February 1981, 3 July 1981, and 11 March 1982 and off of Huntington Beach, CA, on 19 March 1981. The females were separated from the males (easily recognized by their darkly pigmented anal fin and gill membranes) and their eggs stripped into petri dishes filled with seawater. Sperm stripped from the males was then added to selected clutches of eggs while other clutches were left unfertilized. One clutch from the spawn of July 1981 and two clutches from the spawn of March 1981 were split in half and only one-half was fertilized.

The eggs were incubated in natural seawater in a refrigerated 227 L tank with undergravel filter and within a temperature range of 13°-16°C (the March 1981 spawn was kept at 14°-16°C). The egg clutches were kept separate in plastic containers each with its own airstone. For the last spawning, March 1982, the undergravel filter was not used and the gravel removed completely in an attempt to cut

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[2]R. Rosenblatt, Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, pers. commun. winter 1983.

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down on bacterial and nematode infestation. The seawater was initially UV sterilized and filtered before use in the tank. Ten percent of the water was replaced every week.

The developing eggs of the first three spawnings were sampled every 2 hours for the first 12 hours and then only once a day. The eggs of the last spawning, March 1982, were sampled at 16, 38, 63, 89, and 110 hours and 6, 8, and 10 days. Living eggs were illustrated using a Wild M5[3] dissecting microscope with camera lucida. Measurements of egg diameter, perivitelline space, and oil globule diameter were taken with an ocular micrometer.

After hatching the larvae were put into 10 L plastic buckets and later transferred to the main culture tank. Ten percent of the water was changed every day. The larvae were fed the rotifer, *Brachionus plicatilis* (Hunter 1976; Misitano 1978). For the March 1982 spawn the culture tank bloomed initially with algae, including species of *Tetraselmas* and *Isochrysus*. Fresh rotifers and algae were added daily. After 20 days, *Artemia salina* nauplii were added in addition to the rotifers.

The reared larvae were sampled and viewed at hatching and every day thereafter for 12 days, and then less frequently thereafter up to 35 days. A total of 40 larvae were preserved in 4% formalin after being tranquilized with dilute quinaldine. Twenty-five larvae were preserved for analysis of pigment characteristics and morphometric comparison. Length was recorded as notochordal (NL), flexion (FL), or standard (SL) depending on the stage of caudal fin development. Selected sizes of preserved specimens were drawn using the camera lucida.

Field-collected larvae were obtained from the King Harbor Ichthyoplankton collection and the Bightwide Ichthyoplankton Program collection (LACM). Two juveniles (LACM 21639, 43579-1) were obtained from the LACM adult fish collection. Additional specimens were obtained from Marine Ecological Consultants (MEC) of Encinitas, CA. The larva from the King Harbor Ichthyoplankton collection was collected in King Harbor using a single conical 1 m diameter plankton net with 335 μm mesh towed just below the surface (McGowen 1978). A total of 420 larvae was collected by the Bightwide Ichthyoplankton Program along the California coast between Point Conception and the Mexican border using either an Auriga net (benthic sampler) or a 70 cm diameter bongo net for oblique and middepth tows (R. J. Lavenberg pers. commun.[4] and G. E. McGowen pers. commun.[5]). A 16.3 mm juvenile was collected by the Bightwide Ichthyoplankton Program with an Auriga net set with 2 mm diameter mesh. Five specimens from MEC were collected off San Onofre, CA, and the Santa Margarita River, CA, using an Auriga net (W. Watson pers. commun.[6]). Transforming larvae >10.5 mm and <16.3 mm were absent from the above collections.

Sixteen specimens were double-stained for bone and cartilage using alizarin red and alcian blue stains (Dingerkus and Uhler 1977) including one juvenile (LACM 43579-1). Eleven specimens including the juvenile were used for meristic counts.

Field-collected larvae were identified by comparing the pigmentation and myomere counts of smaller size larvae (2.7-5.8 mm) with reared larvae and by comparing larger size larvae (<9.3 mm) with cleared and stained specimens identified using vertebral, dorsal fin, anal fin, and pelvic-fin ray counts. A 10.5 mm larva was identified by meristics, including radiograph vertebral counts, and consistent spine and pigment development. A total of 425 field-collected larvae was examined; 55 larvae and 2 juveniles were observed for detailed pigment characteristics, morphometrics, and meristic counts.

Definition of terms

Preanal length = distance from the snout to a vertical line through the anus.

Body depth = depth of body at the pectoral fin base.

Pectoral fin length = horizontal distance from upper fin base to posterior edge of fin or end of longest ray.

Head length = distance from snout to posterior edge of opercle.

Flexion length (FL) = distance from the snout to the posterior tip of notochord during the stage when the posterior notochord starts to bend upward until the stage when the hypural plates are formed and in their permanent orientation, their posterior edges almost vertical.

Eye diameter = horizontal diameter of eye.

Pectoral insertion = ventral attachment of pectoral fin.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]R. J. Lavenberg, Natural History Museum of Los Angeles County Section of Fishes, 900 Exposition Boulevard, Los Angeles, CA 90007, pers. commun. winter 1982.

[5]G. E. McGowen, Natural History Museum of Los Angeles County, Section of Fishes, 900 Exposition Boulevard, Los Angeles, CA 90007, pers. commun. winter 1982.

[6]William Watson, Marine Ecological Consultants, 531 Encinitas Boulevard, Suite 110, Encinitas, CA 90024, pers. commun. summer 1981.

Trunk = muscular section of body not including the head, abdominal cavity or caudal fin.

RESULTS

Fertilization

Eight whole egg clutches were externally fertilized with freshly stripped sperm, and five contained eggs that developed successfully into the embryo stage. Three whole egg clutches were left unfertilized, and none contained eggs that developed successfully into the embryo stage. Three whole egg clutches were split in half; one half was fertilized with sperm and the other was left unfertilized. Eggs in all three of the fertilized halves developed successfully into the embryo stage; eggs in the unfertilized halves did not. Therefore, there was no evidence of internal fertilization.

Egg Description

Icelinus quadriseriatus eggs are adhesive and negatively buoyant after being stripped from the female and formed a single clutch of 200-250 eggs (excluding eggs that may have been left in the abdomen; Goldberg [1980] reported an average clutch size of 284 eggs in 28 gravid fish). The eggs are 1.08-1.17 mm in diameter and are initially transparent, but the chorion becomes more opaque and textured during development. A pale-green yolk fills most of the egg except for a small perivitelline space (0.024-0.096 mm).

At spawning there are about 15 yellow oil globules, the largest of which is 0.14 mm in diameter, which coalesce to one oil globule of 0.14-0.19 mm diameter by the eighth day of development. An opaque, flocculant mass is suspended in the yolk next to the oil globules.

Embryonic Development

The eggs develop for 12-13 days in 13°-16°C seawater before hatching. Sixteen hours after artificial fertilization the blastodisc is well formed (Fig. 1A). By 38 h the eggs are in the crescent stage of gastrulation (Fig. 1B). The germ ring can be seen making its way around the yolk. At 63 hours somites begin to form along the embryo and the eye capsule is present (Fig. 1C). At 89 hours the heart (Fig. 1D), brain, and otic capsules are visible, and the body is lined with 30 or more myomeres. The heart begins beating after 110 hours, and the vitelline veins can be seen coursing across the surface of the yolk (Fig. 1E). At 6-7 days the anus forms, the eyes become darkly pigmented (Fig. 1F), and the tail begins flexing back and forth. A patch of tubercles forms on the interorbital section of the head and persists until immediately after hatching.

At 7-8 days the embryos develop pectoral buds (Fig. 1G) and melanophores begin forming on the anus and surrounding yolk sac. The eyes turn a metallic green and blood begins circulating through the ventral veins and arteries of the body.

Numerous melanophores cover the yolk sac, anus, and postanal ventral midline (Fig. 1H) in late-stage embryos. The head flattens against the chorion and the tubercles spread from the snout to just dorsal to the otic capsule.

After 10-12 days eggs reared at 13°-16°C begin to hatch.

Description of Larvae

The larvae hatch with the oil globules positioned at the anterior of the yolk sac (Fig. 2A). The yolk is absorbed after 6-7 days. The oil globules disappear along with the yolk in reared larvae; whereas, the oil globule(s) in field-collected larvae move about the abdominal cavity, are fragmented, possibly increase in diameter, or are absent completely (Fig. 2B-C). Evidence of the globule's increase in diameter in the field-collected larvae is found in some specimens (6.1-8.0 mm SL) with oil globules from 0.26 to 0.36 mm diameter, about twice the diameters of oil globules in the eggs and yolk-sac larvae.

The percentage of field larvae with oil globules (based on a subsample of 129 larvae) drops from 93% in larvae with yolk sacs (N = 15) to 70% in larvae <3.5 mm (N = 79) to 45% in larvae 3.6-6.0 mm (N = 20) to 27% in larvae 6.1-8.0 mm (N = 15). Larvae over 8.0 mm possess minute or no oil globules.

Reared larvae hatch at 2.7-3.4 mm NL (after preservation); field-collected larvae are found as small as 2.6 mm. The larvae shorten to a varying degree, depending probably on the reaction to quinaldine and Formalin. Reared larvae shrink 5-17% after anesthesia and fixation.

Myomere counts range from 31-37. Double-stained specimens have vertebral counts of 33-35.

Morphometrics are given in Table 1. From 6.0 to 9.4 mm the larvae become more deep-bodied (27-30% SL) and the head length increases to 34% of the standard length.

A pigmented preanal finfold does not preserve in the field larvae as it does in the laboratory-reared larvae. There is a skin connection between the anus and the rest of the gut, usually with one or more

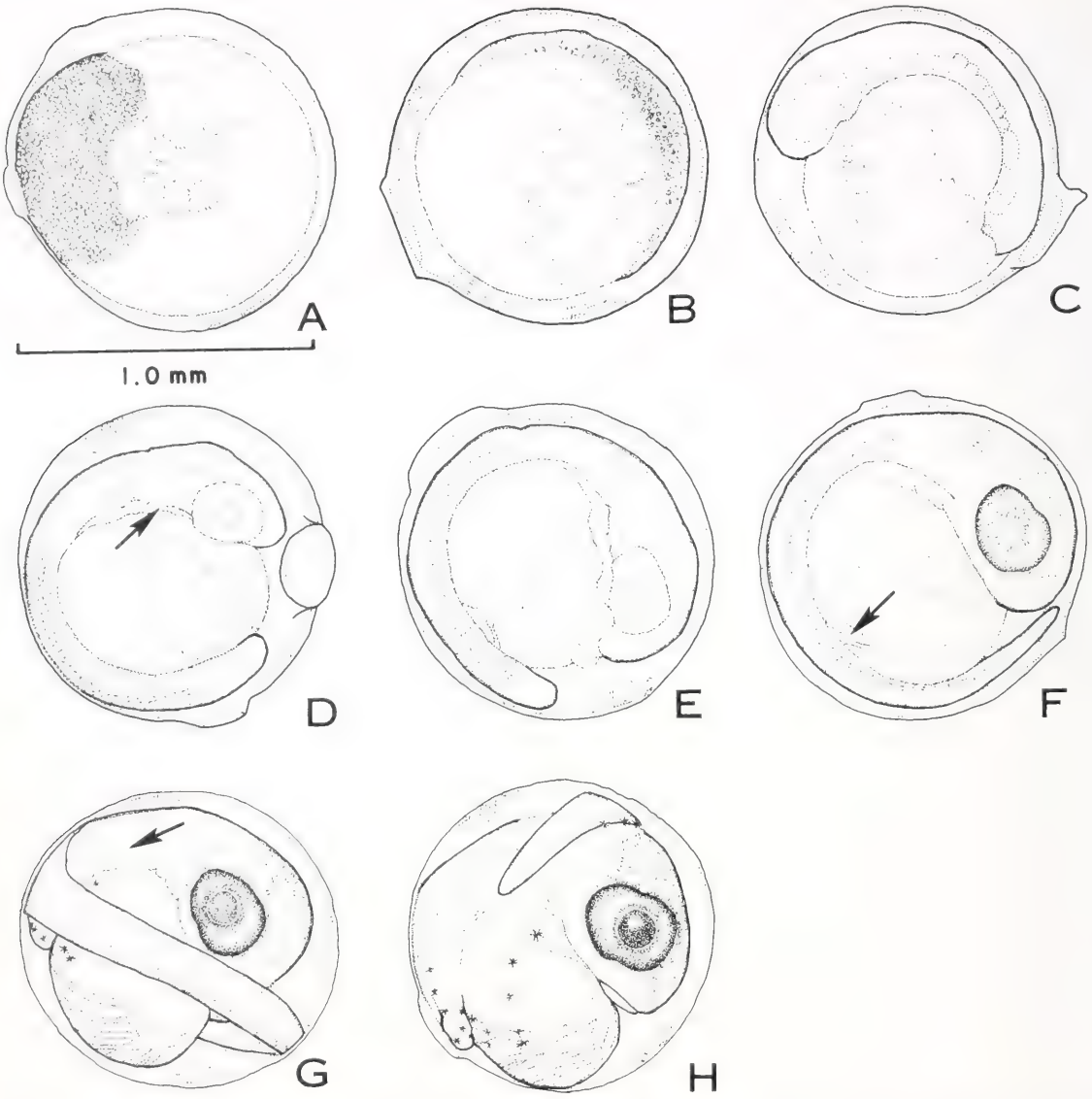

FIGURE 1—Eggs of *Icelinus quadriseriatus*: A) 16 hours (LACM 44159-1); B) 38 hours (LACM 44159-2); C) 63 hours (LACM 44159-3); D) 89 hours (LACM 44159-4), arrow indicates heart; E) 110 hours (LACM 44159-5); F) 6 days (LACM 44159-6), arrow indicates anus; G) 8 days (LACM 44159-7), arrow indicates pectoral bud; H) 10 days (LACM 44159-8).

melanophores, but it is not formed into a finfold as in the reared larvae.

Pigmentation

Pigment in the larvae at hatching is restricted to the postanal ventral midline, the ventral abdominal surface, the dorsoposterior peritoneum, the anus, and the lower jaw angle (Fig. 2A). The postanal ventral midline melanophores are positioned in a single row, number from 25 to 37 in yolk-sac larvae and increase to a maximum of 63 in larvae 3.5-4.0 mm in length. These melanophores decrease to a minimum of 25 in larvae 5.5 mm or larger. The ventral

FIGURE 2.—Field-collected and reared *Icelinus quadriseriatus* larvae: A) 2.8 mm (LACM 025-RB-36-AU-01); B) 3 days old (reared), 3.9 mm (LACM 44160-1); C) 4.6 mm (LACM 012-88-36-BB-01); D) 6.6 mm (LACM 012-88-36-BB-01); E) Ventral view, 6.6 mm.

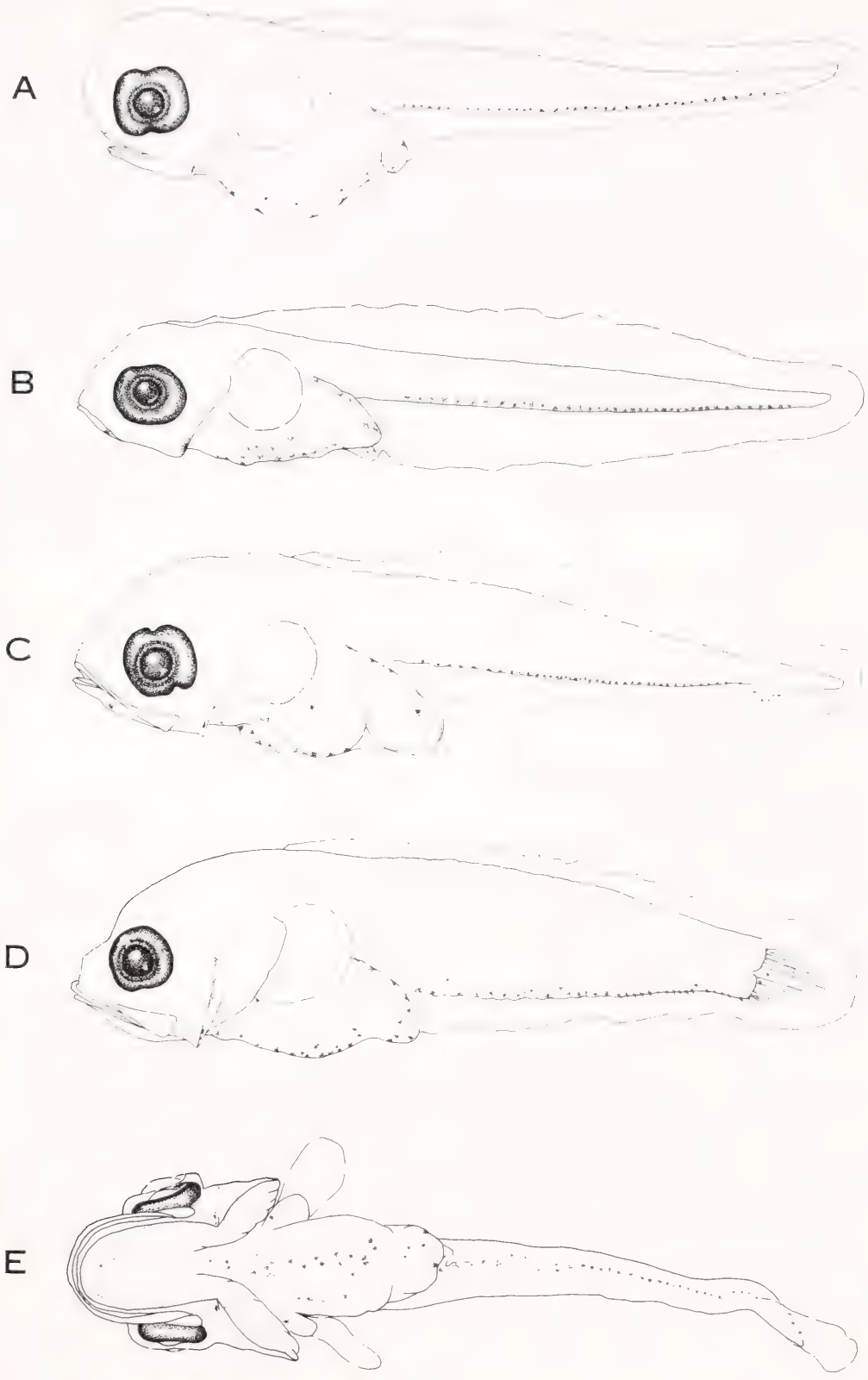
A
B
C
D
E

TABLE 1.—Morphometrics of *Icelinus quadriseriatus* larvae, represented as a mean percentage ($\bar{x}_p$) of body length, with a range (r) of percentages and a standard deviation (SD). Specimens between dashed lines are undergoing flexion of the notochord. * = reared larvae.

Size range (mm)	N	Preanal length			Body depth			Pectoral fin length			Head length			Eye diameter		
		$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD	$\bar{x}_p$	r	SD
2.5-2.9	4	42.0	(38.5-46.1)	4.1	29.6	(25.2-31.9)	3.0	5.9	(5.2-6.8)	0.9	24.0	(20.4-26.2)	2.5	11.3	(9.6-12.2)	1.2
*2.5-2.9	4	47.5	(41.1-51.7)	4.7	25.3	(23.5-27.5)	1.7	8.4	(4.3-13.1)	3.9	25.3	(22.1-28.5)	2.6	12.2	(11.1-14.1)	1.3
3.0-3.4	4	41.2	(39.1-45.0)	2.7	23.8	(21.8-25.5)	2.0	9.1	(7.9-11.0)	1.5	23.0	(21.8-24.7)	1.3	10.9	(10.3-11.3)	0.4
*3.0-3.4	7	45.9	(41.2-51.3)	3.8	21.7	(19.1-24.2)	2.1	9.4	(7.1-12.1)	1.7	23.6	(18.2-26.7)	2.8	11.3	(10.0-12.4)	0.9
3.5-3.9	4	43.0	(41.0-44.0)	1.4	22.9	(21.1-26.6)	2.5	7.4	(6.6-8.7)	0.9	22.8	(21.1-25.1)	1.7	10.2	(9.7-10.9)	0.5
*3.5-3.9	8	39.5	(34.4-50.5)	4.9	19.0	(15.8-28.5)	4.2	10.7	(7.4-16.7)	2.7	21.3	(17.6-31.5)	4.6	9.7	(8.2-13.6)	1.8
4.0-4.4	4	43.0	(40.0-47.5)	3.3	24.9	(21.0-28.2)	3.0	9.3	(7.3-10.3)	1.4	24.5	(23.0-26.1)	1.3	9.9	(9.0-10.8)	0.7
*4.0-4.4	3	39.7	(36.8-43.2)	3.2	20.4	(15.2-25.2)	5.0	10.5	(6.6-14.8)	4.1	23.1	(19.1-26.6)	3.8	9.9	(8.2-11.1)	1.5
4.5-4.9	4	46.0	(41.9-47.8)	3.2	23.8	(22.1-27.3)	2.4	7.4	(6.8-8.0)	0.6	22.4	(19.4-25.9)	2.8	9.3	(8.9-10.0)	0.9
*4.5-4.9	2	45.0	(40.9-49.1)	5.8	24.6	(23.1-26.0)	2.1	12.5	(10.7-14.2)	2.5	27.5	(27.3-27.6)	0.2	11.7	(11.6-11.8)	0.1
5.0-5.4	4	45.6	(44.0-48.7)	2.1	24.9	(21.1-27.7)	2.8	7.4	(5.5-9.2)	1.6	23.4	(20.4-26.2)	2.6	9.1	(8.5-10.0)	0.7
5.5-5.9	4	44.9	(43.6-48.0)	2.1	26.5	(25.3-28.0)	1.2	8.7	(6.5-10.5)	1.7	25.4	(22.5-27.5)	2.3	9.3	(8.7-10.0)	0.6
*5.5-5.9	1	48.6			26.6			14.8			29.7			11.0		
6.0-6.4	4	49.2	(46.1-54.7)	3.7	27.3	(25.9-28.3)	1.4	9.1	(7.5-11.4)	1.8	27.5	(24.4-30.2)	2.4	8.7	(8.3-9.2)	0.4
6.5-6.9	4	46.0	(44.3-49.9)	2.7	27.2	(24.4-31.2)	3.0	11.5	(8.1-15.7)	4.6	29.4	(25.3-33.9)	3.9	8.9	(8.4-9.4)	0.4
7.0-7.4	4	46.7	(44.1-52.2)	3.2	27.8	(25.4-29.1)	1.5	12.1	(9.3-14.9)	2.9	27.9	(24.7-31.5)	2.5	8.8	(8.5-9.2)	0.3
7.5-7.9	3	48.7	(47.0-49.7)	1.5	27.5	(27.2-27.9)	0.4	17.2	(16.3-18.3)	1.0	30.2	(29.5-31.2)	0.9	9.3	(8.7-9.6)	0.5
8.0-8.4	2	50.7	(47.7-53.6)	4.2	29.0	(27.3-30.7)	2.4	19.7	(15.9-23.5)	5.4	29.8	(29.6-30.0)	0.3	9.6	(8.9-10.2)	0.9
8.5-8.9	4	51.5	(49.4-53.2)	1.6	30.8	(27.4-33.9)	2.7	22.3	(21.1-24.2)	1.3	34.4	(32.4-37.3)	2.4	9.5	(8.7-9.9)	0.5
9.0-9.4	4	52.2	(50.9-54.0)	1.3	29.7	(29.3-30.0)	0.3	23.9	(22.5-25.1)	1.2	33.8	(31.1-36.7)	2.3	9.3	(8.7-10.2)	0.7
9.5-10.4	—	—			—			—			—			—		
10.5	1	51.4			25.6			32.2			39.1			11.1		
16.3	1	51.5			22.7			28.8			36.8			11.0		
18.7	1	46.5			26.7			24.6			37.9			9.1		

abdominal pigment consists of 1-6 rows of melanophores aligned anteroposteriorly (Fig. 2E). The dorsal peritoneal pigment consists of 2-5 melanophores in a double row over the posterior half of the gut, increasing to a maximum of 17 in a 5.8 mm reared larva. There are usually 3-5 melanophores surrounding the anus in newly hatched larvae and up to 12 in the larger larvae. There is always a distinct melanophore on the lower jaw angle.

As the larvae grow they develop melanophores on the isthmus (throat), chin, pectoral insertion, anterior gut (usually 2 melanophores slightly internal from the ventral abdomen), head, and dorsal body (Table 2). Reared larvae >4.0 mm possess considerably more pigment (based on the number of melanophores) on the dorsal body and the anterior gut areas than field larvae of the same size.

The larvae undergo flexion between 5.2 mm and 7.6 mm (reared larvae 4.5-5.8+ mm). Melanophores (1-4) are usually present on the caudal fin anlage and later at the base of the caudal fin. In flexion and postflexion larvae the caudal fin base melanophores are present in over 95% of the specimens.

Postflexion larvae (8.0-9.3 mm SL) develop numerous small punctate melanophores over the midbrain portion of the cranium (Fig. 3A). Melanophores form between the otic capsule and the hindbrain. Melanophores occur on the preopercle between the eye and the fourth preopercular spine. There are 1-3 melanophores at the pectoral insertion, 3-6 melanophores along the pectoral base, and a circle of 7-9 small melanophores dorsal to the pectoral origin. There are 4-11 small melanophores ventral to the eye and dorsal to the maxillary bone and 1 melanophore at the posteroventral edge of the maxillary. Several melanophores occur along the edge of the mandible from the articular to the dentary bone. Four to five minute melanophores are situated between the eye and premaxillary bone. The ventral abdomen becomes sprinkled with 40-45 melanophores.

Transition from larval to juvenile pigmentation starts at about 9.2-9.5 mm SL. Transforming larvae develop four patches of melanophores on the dorsal trunk and three patches on the lateral trunk (Fig. 3B). Melanophores appear on the dorsal and caudal fins. In larger specimens (Fig. 3C) the head and dorsolateral pigment takes on the juvenile pattern. The dorsal and lateral trunk melanophores merge forming three dorsolateral bars on the body. Distinct patches of melanophores cover the hypural

FIGURE 3.—Field-collected *Icelinus quadriseriatus* postlarvae and juvenile (D): A) 9.3 mm (LACM 012-88-36-BB-01); B) 9.2 mm (MEC I48 Stn. E Rep. #2); C) 10.5 mm (MEC I-89, E-LS EPI); D) 18.7 mm (LACM 21639).

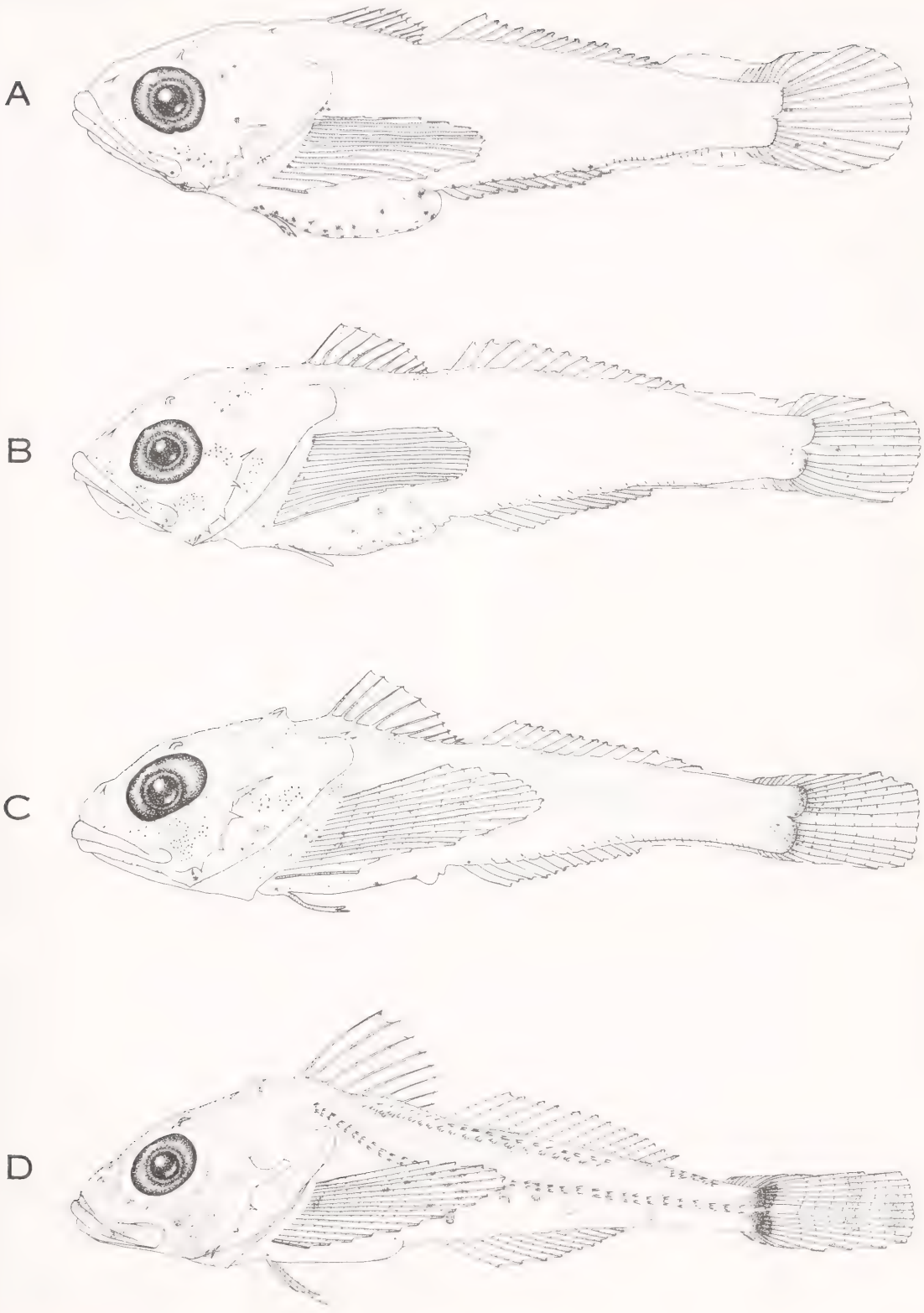
A
B
C
D

TABLE 2.—Presence of melanophores at described locations in *Icelinus quadriseriatus* larvae, represented as a percentage of larvae showing the melanophoes. * = reared larvae.

Size range (mm)	N	Lower jaw angle	Isthmus (throat)	Chin	Pectoral insertion	Anterior gut	Head (dorsal)	Dorsal trunk
2.5-2.9	4	100.0	0.0	0.0	0.0	25.0	0.0	0.0
*2.5-2.9	4	100.0	25.0	0.0	0.0	0.0	0.0	0.0
3.0-3.4	4	100.0	0.0	0.0	0.0	0.0	0.0	0.0
*3.0-3.4	7	100.0	14.3	42.9	14.3	0.0	14.3	14.3
3.5-3.9	4	100.0	75.0	50.0	25.0	0.0	0.0	0.0
*3.5-3.9	8	100.0	75.0	62.5	50.0	12.5	37.5	25.0
4.0-4.4	4	75.0	25.0	50.0	0.0	0.0	0.0	0.0
*4.0-4.4	3	100.0	100.0	100.0	100.0	66.7	33.3	0.0
4.5-4.9	4	100.0	25.0	50.0	0.0	0.0	0.0	0.0
*4.5-4.9	2	100.0	100.0	100.0	100.0	50.0	50.0	50.0
5.0-5.4	4	100.0	50.0	25.0	25.0	0.0	0.0	0.0
5.5-5.9	4	100.0	100.0	0.0	25.0	25.0	0.0	0.0
*5.5-5.9	1	100.0	100.0	100.0	100.0	100.0	100.0	100.0
6.0-6.4	4	100.0	100.0	25.0	50.0	25.0	0.0	0.0
6.5-6.9	4	100.0	100.0	25.0	50.0	0.0	0.0	0.0
7.0-7.4	5	100.0	80.0	40.0	0.0	20.0	0.0	20.0
7.5-7.9	3	100.0	100.0	0.0	66.7	0.0	0.0	0.0
8.0-8.4	2	100.0	100.0	0.0	100.0	0.0	0.0	0.0
8.5-8.9	3	100.0	100.0	66.7	100.0	33.3	33.3	33.3
9.0-9.4	5	100.0	100.0	80.0	100.0	60.0	80.0	20.0

plates. The ventral abdomen and postanal ventral melanophores begin to fade and become less numerous.

Transformed juveniles (including a 16.3 mm specimen, LACM 056-OB-75-JA01) display most adult characters (Bolin 1944) including a double row of scales just ventral to the dorsal fin (Fig. 3D). A gap in the scale row is located below the insertion of the second dorsal fin. Melanophores almost disappear from the postanal and ventral midline and concentrate on the head, dorsal body, and fins. There is a concentration of pigment between the eye and the lower jaw angle and at the base of the caudal fin.

Meristic Elements

Ray elements of the pectoral and caudal fins start developing in larvae 6.8-7.0 mm long. Spine and ray elements of the dorsal and anal fins develop at about 7.4-7.6 mm. The pelvic fin elements are countable in specimens that are double stained and at least 8.2 mm SL (Table 3).

The fin and vertebral counts of 10 double stained field-collected larvae 7.4-8.9 mm long and one juvenile 27.8 mm SL correspond closely to the counts of 36 x-rayed adults from the LACM collection. These counts are consistent with x-ray count frequencies given in Howe and Richardson (1978) except for the dorsal spine counts. The most frequent dorsal spine count listed in Howe and Richardson was eight whereas in the LACM specimens it was nine. It is possible that there is some slight variability in this meristic character or the last (inconspicuous) dorsal spine may have been overlooked in the former's x-ray counts.

TABLE 3.—Meristics of *Icelinus quadriseriatus* larvae. ND = no data (specimens between the dashed lines are undergoing flexion of the notochord). * = reared larvae; + = cleared and stained larvae; ° = x-rayed.

Size (mm SL)	Dorsal fin spines	Dorsal fin rays	Anal fin rays	Pectoral fin rays (left)	Pectoral fin rays (right)	Pelvic fin spines and rays (left)	Pelvic fin spines and rays (right)	Preopercle spines	Precaudal vertebrae	Caudal vertebrae	Total Vertebrae	Myomeres	Postanal ventral melanophores
*2.7	—	—	—	—	—	—	—	—	—	—	—	34	33
3.5	—	—	—	—	—	—	—	—	—	—	—	34	42
4.7	—	—	—	—	—	—	—	—	—	—	—	34	32
+5.3	—	—	—	—	—	—	—	—	—	—	—	34	44
5.7	—	—	—	—	—	—	—	—	—	—	—	36	38
*5.8	—	—	—	—	—	—	—	—	—	—	—	34	34
6.6	—	—	—	—	—	—	—	—	—	—	—	34	34
+6.8	—	—	—	11	11	buds	buds	2	ND	ND	ND	35	26
+7.4	IX	12	11	16	16	—	—	4	10	24	34	ND	30
+7.6	—	—	12	12	14	buds	buds	3	ND	ND	ND	35	27
7.7	IX	14	13	15	16	buds	buds	4	ND	ND	ND	33	28
+8.2	X	15	13	16	16	I,2	I,2	4	11	22	33	ND	34
+8.5	VIII	14	12	16	16	I,2	I,2	4	11	23	34	ND	31
°9.2	IX	14	12	16	16	I,2	I,2	4	ND	ND	34	35	29
°9.3	IX	14	12	16	16	I,2	I,2	4	ND	ND	34	34	32
°10.5	IX	13	12	15	16	I,2	I,2	4	ND	ND	33	33	28
°16.3	IX	14	12	16	16	I,2	I,2	4	11	23	34	ND	8
°18.7	VIII	13	11	16	16	I,2	I,2	4	10	24	34	ND	4

Ossification

Ossification begins in larvae at least 5.3 mm NL long. The cleithrum, premaxilla, maxilla, mandible, parts of the neurocranium, and 3 of 6 branchiostegal rays on each side are ossified. The first 14 vertebrae, the middle 10 out of 12 principal caudal rays, 11-13 pectoral rays, 2-3 preopercular spines, and opercle bone, and all of the branchiostegal rays become ossified at 6.8-7.0 mm.

Ossification is well developed in specimens 7.4 mm FL long or greater. The nasal, quadrate, dorsal spines, and the first 28 of 33 vertebrae become ossified as well as the hypural plates and all of the principal caudal rays.

A double row of teeth appears on the lower jaw of double-stained larvae between 6.8 and 7.4 mm FL in length. On the upper jaw a single row of teeth is seen in larvae 8.5 mm SL or greater in length.

Spination

One to three preopercular spines appear at 6.5-7.0 mm FL. Four preopercular spines are visible in larvae over 7.0 mm FL. Nasal and parietal spines form at 9.0-9.3 mm SL. Double-stained material shows the parietal spine arising from two arcs of bone that fuse distally into one spine before breaking the surface of the skin. A foramen remains in the center of the spine and is retained in the parietal spines of juveniles and adults.

Development of the Caudal Complex

The caudal fin anlage begins to form in preflexion larvae of about 5.3 mm NL (Fig. 4A). During flexion three non-ossified hypural elements form ventral to the notochord (Fig. 4B). The first hypural (identified as HY_{1-3}) may be a remnant of a fusion process of two to three elements. Matarese and Marliave (1982) described three elements that fuse to form the inferior hypural plate in *Ascelichthys rhodorus*; a foramen is left where the parhypural (counted as HY_1) fuses with HY_2 and HY_3. In *I. quadriseriatus* a foramen is present in HY_{1-3}.

The second and third hypural elements (HY_4 and HY_5) form separately (Fig. 4B-C) and fuse to form the ossified superior hypural plate (HY_{4-5}) (Fig. 4D). Finally, the two plates (HY_{1-3} and HY_{4-5}) begin to fuse anteriorly in juveniles (Fig. 4D).

Cartilaginous neural spines begin to form during flexion (Fig. 4B). By about 8.7 mm SL the neural spine on the first preural centrum (PU_1) appears (on one specimen) as two distinct elements (Fig. 4C).

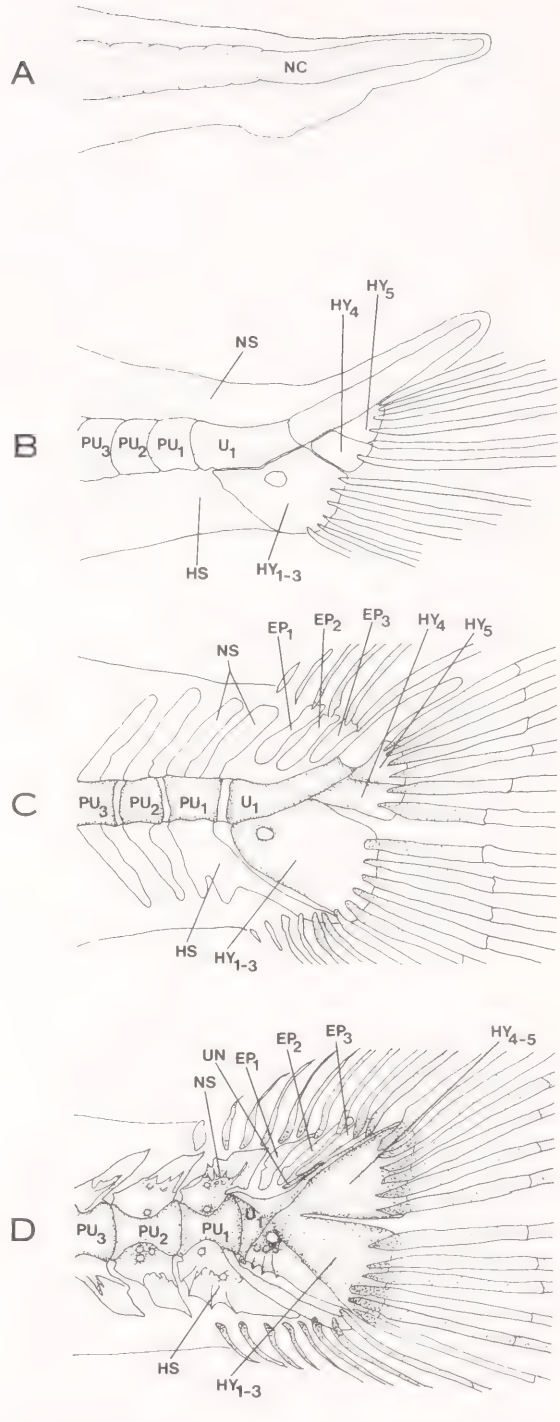

FIGURE 4.—Caudal complex of *Icelinus quadriseriatus*: A) 5.3 mm (LACM 012-88-36-BB-01); B) 6.8 mm (LACM 012-88-36-BB-01); C) 8.7 mm (LACM 012-88-36-BB-01); D) 27.8 mm (LACM 43579-1). EP = epural; HS = hemal spine; HY = hypural; NC = notochord; NS = neural spine; PU = preural centra; U = urostyle; UN = uroneural.

This condition has been illustrated in one other larval sculpin (Matarese and Marliave 1982, Fig. 2E), but may be variable. By the juvenile stage the neural element(s) appear as one broad, ossified spine (Fig. 4D).

Hemal spines form in unison with the neural spines. The hemal spine on the first pre-ural centrum develop an elongate, descending process to which several procurrent rays articulate. A similar elongate structure was identified as the parhypural in *Icelus spiniger* (Nelson 1984). The present study agrees with Materese and Marliave (1982) and Yabe (1985) in identifying the process as part of the hemal spine because it is always associated with the spine during development.

Twelve principal caudal rays develop and articulate with the hypural plates during flexion (Fig. 4B). The number of these rays varies in other sculpins from 11 to 13 (Materese and Marliave 1982; Nelson 1984).

Procurrent rays form after flexion (Fig. 4C) and increase in number to a maximum of 10 for the upper procurrent rays and 8 for the lower procurrent rays. The last lower procurrent ray appears to articulate with a radial cartilage between the posterior tip of the descending hemal spine process and the anteroventral edge of the inferior hypural plate.

Three epurals form dorsal to the ural-centrum in the postflexion larvae and are also present in juveniles and adults. A uroneural appears dorsal to the reduced urostyle in the juveniles (Fig. 4D).

Occurrence

Icelinus quadriseriatus larvae were collected in every month of the year with peak occurrence from May to June in 1979, which is in agreement with peak occurrence of prespawning females (Goldberg 1980) for 1977, allowing for a time lag between prespawning condition and hatching of the larvae; the larvae are assumed to be planktonic for about 2 months. Peak spawning periods may vary yearly. Goldberg (1980) reported a winter peak of oocyte development that was earlier in 1978 (January-April) than in 1977 (March-June).

In the Southern California Bight, *I. quadriseriatus* larvae seemed to be concentrated in deeper waters away from the intertidal and shallow subtidal areas. Of the 33 bightwide discrete depth samples (nueston, middepth, and epibenthic) collected in 1979 in which *I. quadriseriatus* occurred, only 2 samples were taken at the 8 or 15 m depth stations. Ten samples were taken at the 22 m stations and 21 samples were taken at the 36 m station.

Icelinus quadriseriatus larvae were generally found near the bottom of the water column. Of the 33 discrete depth tows taken in which *I. quadriseriatus* larvae were found, 31 were epibenthic tows and two were middepth tows.

The bottom temperature at stations where *I. quadriseriatus* larvae occurred ranged from 11° to 14°C. Since the larvae were usually found at the bottom, this suggests that these are the temperatures under which they normally develop in the field. Reared larvae were observed to survive aquarium temperatures of at least 18°C.

DISCUSSION

Fertilization

Many cottids, including *Chitonotus* and *Oligocottus snyderi*, practice internal fertilization facilitated by an intromittent male sex organ (Morris 1956; Hubbs 1966; Stein 1973; Misitano 1980). Bolin (1941) reported that *Orthonopias triacis* has internal fertilization even though the males do not have an external penis. Apparently the female has a "protrusile oviduct" which is probably smeared with sperm and then retracted. Fertile eggs have been removed from females of *Scorpaenichthys marmoratus* and *Icelinus filamentosus* (Hubbs 1966). *Icelinus quadriseriatus* males possess no external penis and since no females were found with fertile eggs, it is still questionable as to what mode of fertilization these sculpins possess. It is possible that *I. quadriseriatus* has external fertilization (a rarity among sculpins), but until the mating process is observed or an internally fertilized female is found, this question will remain unanswered.

Comparison with Other Sculpin Eggs

The eggs of *I. quadriseriatus* are adhesive, demersal, and share many characteristics with other cottid eggs. The presence of a flocculant mass inside the yolk has been observed in several other genera such as *Chitonotus*, *Orthonopias*, *Clinocottus*, and *Leptocottus* (Bolin 1941; Morris 1951; Jones 1962; Misitano 1980). Multiple oil globules that coalesce to one globule are common in other sculpins; however, *I. quadriseriatus* does have the highest initial number of oil globules (15) recorded in the literature. The diameters for *I. quadriseriatus* eggs are closest to the diameters of *Artedius lateralis* and *Clinocottus analis* eggs (Budd 1940).

The pale-green color of the yolk and the pigmentation of the late-stage embryo are most similar to

Chitonotus pugetensis eggs (Goldberg 1980; Misitano 1980). (The eggs of other *Icelinus* species have not been described and could not be used for comparison.)

The appearance of tubercles on the head of the late-stage embryos has been observed in several other cottid species. Budd (1940) described them in *Artedius lateralis* and *Clinocottus analis* as a "patch of minute nodules" which are "believed to aid as a rasp in breaking through the shell. . . allowing the larva to escape anterior end foremost". Bolin (1941) referred to them in *Orthonopias* as a "large number of small granular patches". Morris (1951) described them in *Clinocottus recalvus* as "minute convexities of low elevation which grade into the dorso-anterior surface of the head" and are formed due to the "the extreme pressure which it suffers during its late stages of confinement". In the case of *I. quadriseriatus* the head does flatten in the late-stage embryos and may be under pressure, but whether these structures form in response to that pressure is not known. The tubercles may serve only to reinforce the area of the head which pushes its way through the chorion.

Distinguishing Larval Characters

Distinguishing characters include 1-6 rows of ventral gut melanophores, 25-63 postanal ventral melanophores, and a distinct lower jaw angle melanophore on either side. An increasing percentage (25-100%) of larvae over 3.5 mm in each size class develop isthmus, chin, and pectoral insertion melanophores.

Icelinus quadriseriatus larvae are characteristic of the *Paricelinus/Triglops/Icelus/Chitonotus/Icelinus* group of Richardson (1981) which is distinguished by four preopercular spines, a pointed snout, moderately slender body, and postanal pigment restricted to ventral midline.

Paricelinus, *Triglops*, and *Icelus* all have a higher number of vertebrae: 40-42, 44-54, and 37-44 respectively (Washington et al. 1984), than *I. quadriseriatus*. *Paricelinus hopliticus* in addition has pigment on the snout, nape, and anterior gut in preflexion larvae.

Chitonotus pugetensis larvae, while similar in appearance to yellowchin larvae, differ in having several anterior gut melanophores, an early development of head pigment and a slightly higher range of vertebrae (35-36). Larger (6.0-9.4 mm) *C. pugetensis* are more slender-bodied (23-25% SL) (Richardson and Washington 1980) than *I. quadriseriatus* SL (27-30%). In transforming *C. pugetensis* larvae there are usually three pelvic fin rays and a nuchal spine next to the parietal spine while *I. quadriseriatus* has only two pelvic rays and no nuchal spine. The fin ray counts of *C. pugetensis* (Howe and Richardson 1978) are somewhat higher than the yellowchin, especially the anal fin rays (14-17, x = 15.7, in *C. pugetensis*; 10-13, x = 12.1, in *I. quadriseriatus* larvae).

Artedius creaseri and *A. meanyi*, recently added to this group (Washington 1986), have anterior gut pigment, pigment in the ventral finfold and fewer postanal ventral melanophores (<13). Postflexion *A. creaseri* and *A. meanyi* larvae have nuchal spines next to the parietal spines.

Seven species of *Icelinus*, all with undescribed larval stages, co-occur with *I. quadriseriatus* in the Southern California Bight, including one undescribed species (R. Rosenblatt fn. 2). Several larvae have recently been collected at a 75 m depth station (LACM) that are very similar to field-collected *I. quadriseriatus* larvae including possession of lower jaw angle, chin, isthmus, and pectoral insertion melanophores. A cleared and stained specimen has a count of 38 vertebrae that identifies it tentatively as *I. tenuis*. These larvae differ from *I. quadriseriatus* in having a higher myomere count (37-40), anterior peritoneal pigment similar to *Chitonotus*, and an absence of caudal melanophores.

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FEEDING ECOLOGY AND GROWTH ENERGETICS OF LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

GAIL H. THEILACKER[1]

ABSTRACT

The relation between prey consumption and gross growth efficiency was determined for first-feeding northern anchovy, *Engraulis mordax*, fed rotifers for 2 weeks. Larval length- and weight-specific daily consumption, given as prey numbers, dry weight, and caloric value, were less for the 2/mL rotifer diet and gut residence time was longer, resulting in a higher gross growth efficiency (0.46) than the 25/mL rotifer diet (0.37). Daily percent increases in dry weight for northern anchovy fed rotifers were 15% at the low density and 21% at the high density. Northern anchovy grew the most, 23% per day, when fed 2/mL copepods, but their length-specific weight was less than those fed on the rotifer diets. Equations for the rotifer and copepod diets are given for calculating growth in length and weight, size-specific stomach contents related to feeding period, and daily food consumption based on empirically determined gastric evacuation rates. Respiration was measured directly and indirectly, by using a starvation analysis to measure the caloric equivalent of metabolism; results from both methods agreed. A power equation was used to express metabolism as a function of dry weight. Estimates of gross growth efficiencies showed that larval northern anchovy may exhibit a high growth rate or a high efficiency, but not both at the same time. Information also is given on increase in size of prey selected as northern anchovy larvae grow.

Measurements of gross-growth efficiency (calories of growth/calories consumed) of fishes are a good indicator of the adequacy of their diet and state of health (Brett and Groves 1979). Generally a favorable environment for larval fish growth can be inferred by using information on growth efficiencies as related to prey densities. A high-growth efficiency is the result of efficient assimilation of food energy for growth, with relatively little energy lost as feces or used in respiration.

A wealth of information is available on larval northern anchovy, *Engraulis mordax*. Research has been directed toward understanding the factors that affect their survival, yet no information exists on the growth efficiency of larval northern anchovy.

Larval northern anchovy have been cultured in the laboratory, and their growth and survival on wild plankton (Kramer and Zweifel 1970; O'Connell and Raymond 1970) and on cultured foods (Lasker et al. 1970; Theilacker and McMaster 1971; Hunter 1976) have been described and compared with their growth in the field (Methot and Kramer 1979). Incubation times, yolk absorption and the onset of feeding (Lasker 1964; Lasker et al. 1970), feeding success and swimming behavior (Hunter 1972) and their ability to withstand starvation (Hunter 1976; Theilacker and Dorsey 1980) have been studied. Here I describe how variations in prey density affect consumption, growth, and gross growth efficiencies and compare my results to those on other larval fishes.

MATERIALS AND METHODS

The rationale for my experimental design was to avoid known problems that affect interpretation of results of energetic studies. Mainly I determined gut contents directly, which gives a measure of individual variability, rather than by controlling prey level in the tank and estimating feeding by difference in prey numbers over time. To obtain more precise fresh dry weight values for these small larvae, I grouped them by size class to increase the measured weight. I converted the number of prey eaten to width-specific and species-specific fresh dry weights and caloric values, thus precluding problems inherent with feeding rate estimations that use preserved sample weights and/or average prey weights. Because gastric evacuation depends on feeding rates, I conducted the evacuation experiments with actively feeding larvae. In addition, I compared and validated traditional oxygen uptake measurements with a starvation analysis used to estimate the caloric equivalent of metabolism.

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Larval Rearing

Northern anchovy eggs were spawned by administering hormone injections to a brood stock held at the Southwest Fisheries Center (Leong 1971). Larvae raised from the eggs were kept in 100 L circular, black polypropylene tanks at constant temperature (15.5°C) and photoperiod (12 h/12 h). In this study, I varied the prey type and density. At the onset of feeding, northern anchovy larvae have small mouths that restrict their feeding to small prey (Hunter 1977). Thus for the initial feeding (day 3) all larvae were fed *Gymnodinium splendens*, a naked dinoflagellate having a width of about 50 μm (Lasker et al. 1970), and 2 days later the larvae were fed larger prey. Because it is impossible to quantify the caloric input from *Gymnodinium* directly (digested cells cannot be counted), the experiments began on day 5 when the larger prey could be removed from the fish stomachs, counted, measured, and subsequently expressed as caloric input.

Experimental Design

I conducted five experiments. In the first experiment, rotifers, *Brachionus plicatilis*, at a density of 35/mL were fed for 20 days, and the number of prey eaten was determined. The size of the rotifers was not measured in this initial experiment, but in subsequent experiments, widths of prey eaten were measured. In the second and third experiments, rotifers were offered at densities of 2 and 25/mL respectively for 14 days. In the fourth experiment, copepods, *Tigriopus californicus*, nauplii and copepodites were fed to larvae at a density of 2/mL (usually 1 nauplius and 1 copepodite/mL) for only 9 days instead of 14 days because of problems with the copepod culture. In the fifth experiment, larvae were fed copepods at 0.2/mL for 12 days without the initial addition of *Gymnodinium*. (Mortalities were high on this low density copepod diet, and data are few; high mortalities are consistent with results reported by O'Connell and Raymond [1970] for northern anchovy raised on a similar diet. The addition of a *Chlorella* bloom to this diet improves survival of northern anchovy [Moffatt 1981].)

To estimate larval growth as the increase in standard length, SL, and dry weight, W, larvae were pipetted individually onto a slide and measured while alive. Larvae were then rinsed in distilled water and, to ensure dependable mean dry weight determinations, grouped by size class onto a clean slide. Larvae <5 mm were grouped by 0.2 mm size class, and those >5 mm were grouped by 0.3 mm size class. Numbers of larvae per group ranged between 2 and 12; the larger the larval weight, the fewer larvae I grouped together. After drying to a constant weight at 60°C (Lovegrove 1966), larvae were removed from the slides by using a single-edged razor blade and weighed on a Cahn electrobalance to ±2 μg.

Feeding

To estimate feeding rates and daily consumption, each prey item removed from the larva's gut was counted and its width measured. Width is the dimension that limits a fish larva's selection of prey (Beyer 1980; Hunter 1981). Prey defecated onto the slide were included in the total number eaten. Gut contents in dry weight were determined by summing the width-specific weights of the prey eaten each day. I used the width-specific fresh dry weights and caloric values for *Brachionus* and *Tigriopus* given by Theilacker and Kimball (1984) and reproduced here in Table 1.

Because northern anchovy larvae eat continuously, asymptotic curves ($c = C_{max} \times (1 - e^{-kt})$) were used to describe food intake, i.e., the relation between observed gut contents c and time t, where C_{max} is the asymptotic gut contents (contents in gut at steady state after filling) and k is the instantaneous rate of gut filling. Using Marquardt's algorithm for fitting nonlinear models, parameters C_{max} and k were estimated for 0.5 mm length classes (Table 2). Fish with empty stomachs were included in this analysis because all fish were used in the growth estimates. Daily mean gut contents $\bar{c}$ were calculated by integrating the area beneath

TABLE 1.—Width-specific dry weight and caloric value of rotifers, *Brachionus plicatilis*, and copepods, *Tigriopus californicus*[1].

Prey	Width class μm	Per individual: Dry weight μg (SE)	Per individual: Volume × 10^6 μm	Per individual: Caloric value × 10^{-3} cal
Brachionus plicatilis (4.4 cal/mg)				
Rotifers	74.3-109.7	0.10 (0.01)	0.65	0.44
	109.8-146.7	0.22 (0.04)	1.73	0.97
	146.8-183.8	0.41 (0.06)	2.96	1.80
	183.9-195.0	0.47 (0.08)	3.99	2.07
Tigriopus californicus (4.9 cal/mg)				
Nauplii	74.3-109.7	0.04 (0.01)	0.20	0.20
	109.8-146.7	0.13 (0.01)	0.55	0.64
	146.8-183.8	0.25 (0.01)	1.17	1.23
	183.9-195.0	0.38 (0.00)	1.77	1.86
Copepodites	146.8-183.8	0.63 (0.15)	3.38	3.09
	183.9-221.0	1.20 (0.26)	6.21	5.88

[1]From Theilacker and Kimball 1984, table 2.

TABLE 2.—Estimates of the asymptotic gut contents (C_{max}) and instantaneous rate of gut filling (k) for northern anchovy (n) fed several diets[1].

Diet	Prey level per mL	SL (mm)	n	Prey number C_{max}	Prey number k	Prey weight µg C_{max}	Prey weight µg k
Rotifers[2]	35	4.00	89	6.16	0.33		
		5.00	236	9.90	0.32		
		6.00	131	11.91	1.13		
		7.00	219	15.92	3.73		
		8.00	159	28.33	3.78		
		9.00	171	46.36	2.56		
		10.00	89	52.22	1.72		
Rotifers	25	4.25	58	[3]15.55	0.12	1.80	0.29
		4.75	69	7.79	0.67	2.12	0.67
		5.25	54	12.93	0.62	2.36	0.83
		5.75	35	14.01	0.64	2.92	0.58
		6.50	28	16.97	1.96	3.31	3.76
		8.00	32	27.80	1.84	6.68	1.61
Rotifers	2	4.25	33	7.44	0.35	0.50	0.18
		4.75	19	4.97	1.61	1.35	0.98
		5.25	18	8.86	1.29	2.42	0.73
		8.00	16	9.94	1.30	4.00	0.88
Copepods[4]	2	4.25	21	1.54	1.27	0.08	0.49
		4.75	63	4.89	0.42	0.52	0.37
		5.25	44	4.45	0.45	0.94	0.57
		5.75	32	3.86	0.41	1.15	1.49
		[5]6.25	31	4.94	1.01	1.99	0.86
		8.00	14	7.22	1.30	3.66	0.66

[1]Includes zero gut contents; observed gut contents c at time $t = C_{max} \times (1 - e^{-kt})$.
[2]Prey width not measured.
[3]87% rotifers <150 µm width.
[4]Fish eating *Gymnodinium* exclusively were removed to estimate C_{max} and k.
[5]Copepod concentration <0.1/mL.

the curves and dividing by the 12-h feeding period.

Equations were derived for each diet from the relation of C_{max} and k with fish size and duration of feeding; these equations allow the calculation of gut contents c at time t for all fish lengths between 4 and 8 mm. The parameters (Table 3) were found using the derivative-free nonlinear regression program (BMDPAR) by Biomedical Computer Programs (BMDP, 1981).

Daily consumption F_w was estimated using a modification of an equation for consumption developed by Stauffer (1973) and discussed by Elliott and Persson (1978) and Jobling (1981), $F_w = rt + C_{12}$, where r is the µg evacuated per hour calculated as mean gut contents $\bar{c}$ divided by the empirically determined rate of gastric evacuation (see Evacuation Rates), t is the duration of feeding, and C_{12} is the dry weight of the food remaining in the stomach at the end of the 12-h feeding period.

Growth

Length data for all feeding treatments were fit to exponential growth curves, $SL = l_0 e^{kt}$ where l_0 is length at hatching, k is the instantaneous growth rate and t is the age. Length-weight data were fit to a power equation where weight $W = a(SL)^b$; parameters for the growth equations are given in Table 4.

TABLE 3.—Parameters for equation[1] relating observed gut contents c in µ g dry weight at time t to standard length (SL) of northern anchovy fed three diets.

Diet	Age	n	P_1	(SD)	P_2	(SD)	P_3	(SD)	P_4	(SD)
Rotifers										
25/mL	5-14	280	−1.90	(0.70)	0.51	(0.18)	0.57	(0.16)	0.29	(0.03)
2/mL	5-14	103	—	—	[2]0.69	—	0.33	—	0.326	—
Copepods										
2/mL	5-9	171	2.84	(0.88)	−0.39	(0.12)	[3]1.26	[3](0.75)	1.18	(0.10)

[1]$c = p_3 e^{p_4 SL \cdot (1 - e^{-(p_1 + p_2 \cdot SL)t})}$.
[2]$(P_1 + P_2)$ fixed at 0.69, the mean k from Table 2; asymptotic standard deviations could not be computed because k was held constant.
[3]$\times 10^{-3}$.

TABLE 4.—Parameters for northern anchovy growth equations where SL is standard length in mm, W is weight in µg, and t is age in days.

Diet	Age (d)	Age length $SL = l_0 e^{kt}$ n	l_0	(SD)	k	(SD)	Length-weight $W = a(SL)^b$ n	a	(SD)	b	(SD)
Rotifers											
25/mL	5-14	280	3.06	0.05	0.06	0.001	253	0.197	0.040	3.16	0.11
2/mL	5-14	103	3.14	0.07	0.05	0.002	84	0.379	0.030	2.80	0.04
Copepods											
2/mL	5-9	138	3.06	0.15	0.07	0.010	109	0.297	0.097	2.88	0.20

Metabolism

I determined metabolic rates for the larvae, which ranged in age from first-feeding (3 days after hatching) to 25 days using the Winkler technique. I chose the Winkler technique where large vessel volumes could be used and there was no need to shake the vessels during the experiment, as required for manometric techniques. Pearcy et al. (1969) found no differences between Winkler and Warburg estimates of oxygen consumption. Oxygen consumption was estimated at 16°C during 18-23 h experimental periods with a 12 h light-dark cycle. The respiration vessels were attached to a large, slowly rotating wheel. Young larvae, 0.02-0.14 mg dry weight were tested in 40 mL vessels in groups of 10-50, while larvae older than 16 days (larger than 0.14 mg) were tested individually in 60-150 mL vessels. All fish tested had empty guts. Data were not used when mortalities occurred during the experiment.

To express metabolism (Q) as a function of dry weight, I used a nonlinear regression to fit a power equation to the data (see parameters for Model 1 in Table 5). The data points were weighted by their sample size (n = 10-50). The Model 1 fit was unsatisfactory for the whole size range, presumably because each data point for the young larvae (n = 72) was a group mean, and the model was significantly weighted toward the young larvae, causing it to overestimate oxygen consumption for the few large larvae (n = 17). Because the experimental technique differed (i.e., respiration was measured for groups of young larvae or individual older larvae), I also fitted two separate curves. These curves (Model 2) gave a good fit to the data (Table 5); the Model 2 equation for younger larvae was used in the present study.

An alternate approach for estimating metabolic requirements is to starve larvae of known size (weight), determine the size-specific weight loss, and convert the weight loss to calories. This approach eliminates the need to restrict larval swimming activity in a respiration vessel. Presumably the weight loss in caloric units would equal the loss due to metabolic costs, excluding the metabolic cost of attacking prey. Using this approach, I fed control northern anchovy larvae ad libitum on *Gymnodinium* and *Brachionus* and starved the test larvae; both groups were maintained in 100 L rearing tanks at 15.5°C. Live standard length and dry weight of groups of the same length were measured daily, as described earlier in this Methods section, for 10-50 larvae sampled daily from each treatment.

I calculated the caloric equivalent of northern anchovy tissue using the caloric values given by Hunter and Leong (1981) for fat-free anchovy tissue, 4.129 cal/mg, and for anchovy lipid, 9.227 cal/mg. For example, northern anchovy larvae weighing 25 μg contained 6 μg of lipid (unpubl. data: John Hakanson, UCSD, Scripps Institution of Oceanography); using the above caloric equivalents for 19 μg of fat-free tissue and 6 μg of lipid yields 5.36 cal/mg as the energy equivalent of anchovy tissue. In a 20-d laboratory experiment, Hakanson found that lipid weight appeared to increase proportionally with anchovy weight, thus the caloric content of anchovy tissue would be approximately constant for the age range studied. Lipid content seems to be lower in older northern anchovy larvae. The only other information I found was for 40-60 d-old northern anchovy where the caloric content averaged 4.9 cal/mg (unpubl. data: John Hunter, Southwest Fisheries Center). I used 5.4 cal/mg as the caloric value of anchovy tissue for larvae between 5 and 14 days of age.

TABLE 5.—Parameters for equation $Q = aw^b$ where Q is metabolic rate in μL O_2/h for northern anchovy and w is their fresh dry weight.

Model	N	Size group (mg dry wt) w	Parameters a(SE)	b(SE)
1	89	0.02-2.70	[1]3.844 ± 0.100	0.858 ± 0.029
2	72	0.02-0.14	2.897 ± 0.344	0.834 ± 0.057
2	17	0.14-2.70	4.269 ± 0.325	0.697 ± 0.107

[1]The sum of the residuals in Model 1 does not equal zero, thus the program calculation of SE's is biased.

Evacuation

Gut clearance times were determined for actively feeding fish of various ages fed the rotifer and copepods diets. Larvae were transferred from the 100 L rearing tank to a 10 L test tank. Because northern anchovy larvae are sensitive to handling, handling was restricted to one transfer. Transferred larvae were kept in the test tank for 18 hours prior to an evacuation experiment because injured larvae usually die within 8-10 hours after transfer. First, larvae were fed a low concentration of prey that had been dyed with National Fast Blue (Laurence 1971). After larvae had filled their guts, eating most of the dyed prey, a known density of undyed prey was added. Larvae were sampled at 5-min intervals, and the time required for them to void their guts of the dyed prey was determined. The number of prey in the full guts was counted and converted to dry weight. Evacuation rates are given as μg prey cleared through the gut per hour. Rates were related to fish size and to prey type.

The timing of the second prey addition was not critical for determining gut clearance rates at high prey densities. But when the timing was not correct for the tests that used low prey concentrations, deciphering the meaning of the gut contents was problematical. Results from most of these low-density tests could not be used.

A series of evacuation experiments also was conducted with nonfeeding northern anchovy that were removed from their food source, rotifers, to filtered seawater.

To reduce the incidence of injury during transfer, I constructed a cylindrical, clear plastic container (15 mm high and 7 mm diameter) with handle and a removable bottom grooved to fit the circumference of the cylinder. Larvae to be transferred were surrounded by the cylinder, and then the bottom was fitted onto the cylinder. The container with fish was transferred and lowered into the test tank. Removing the bottom and slowly raising the cylinder released the fish. Prey that were transferred into the experimental tank with the larvae were removed by an air-lift pump that slowly recirculated water and was screened to prevent the removal of larvae (O'Connell and Paloma 1981).

Growth Efficiency

To determine growth efficiencies, I used the information on growth (Table 4), daily food consumption estimated from the general equations (Table 3) and evacuation rates of 1.15 hours for the high-density rotifer diet and 1.5 hours for the low-density diet. Gross growth efficiency was estimated based on dry weight and on caloric estimates. It is the ratio of growth to ingestion. To estimate assimilation efficiency, I used the information on weight-specific metabolic rates and simply combined the energy of metabolism and growth and divided it by the energy consumed. Assimilated energy lost as feces and urine was not accounted for.

RESULTS

Feeding

Sizes of prey fed to larval northern anchovy in these experiments ranged from 50 μm for *Gymnodinium*, to 74-195 μm for rotifers and copepod nauplii, and 147-221 μm for copepodites. In contrast to larvae fed the rotifer diets, fish offered the copepod diet did not switch from eating *Gymnodinium* at first feeding on day 3 to eating larger prey on day 5. All fish fed copepods and sampled on day 5 contained *Gymnodinium* in their gut, and 96% of these guts were full of *Gymnodinium* (Table 6). By day 7, the number of copepod-fed northern anchovy eating *Gymnodinium* had decreased to 80%, with 10% full. These data reveal that young northern anchovy were unsuccessful at capturing *Tigriopus* nauplii at 1/mL until 7-8 days of age, and because of this behavior and the failure of the copepod culture on day 9, I was unable to quantify daily consumption for northern anchovy fed copepods.

Northern anchovy reared on the low-density (2/mL) and high-density (25/mL) rotifer diets ate only a few *Gymnodinium* cells after day 4. Between rotifer treatments, incidence of feeding on *Gymnodinium* after day 4 was higher for fish fed the low-density diet (Table 6). On day 5, northern anchovy concentrated on eating rotifers in the 75-150 μm size range; between 84 and 97% of the rotifers eaten by larvae sampled from both rotifer treatments were <150 μm width (Table 7). Only 7% of the rotifers available to these larvae were smaller than 150 μm width. Hence on day 5 larvae were selecting small rotifers in higher proportions than were available; in the two treatments, the apparent density of roti-

TABLE 6.—Presence of *Gymnodinium* in guts of larval northern anchovy related to age of larvae and to diet.

	Diets								
	Rotifers 25/mL[1]			Rotifers 2/mL[2]			Copepods 2/mL[3]		
Age (d)	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]	*n*	Incidence (%)[4]	Gut full (%)[5]
5	21	48	0	29	83	0	27	100	96
6	82	59	0	11	9	0	57	77	16
7	10	10	0	5	0	0	49	80	10
8	75	9	0	0	—	—	5	0	0
9	27	7	0	38	6	0	33	0	0

[1]Apparent density of rotifers <150 μm = 2/mL.
[2]Apparent density of rotifers <150 μm = 0.1/mL.
[3]Apparent density of nauplii <150 μm = 1/mL.
[4]Percent of larvae having *Gymnodinium* cells in guts with rotifers or copepods.
[5]Percent of larvae having guts full with *Gymnodinium* cells.

TABLE 7.—Width frequency of prey eaten by northern anchovy (n) related to their diets and to their age and size.

Age (d)	Rotifers 25/mL[1] Prey composition (%)			Rotifers 2/mL[2] Prey composition (%)			Copepods 2/mL[3] Prey composition (%)		
	n	<150 μm	>150 μm	n	<150 μm	>150 μm	n	<150 μm	>150 μm
5	21	83.5	16.5	29	97.3	2.7	27	88.0	12.0
6	82	11.0	89.0	11	75.0	25.0	57	60.0	40.0
7	10	5.2	94.8	5	38.7	61.3	49	59.0	41.0
8	75	33.1	66.9	0	—	—	5	33.4	56.6
9	27	40.9	59.1	38	12.2	87.8	33	31.8	68.2
Length (mm)									
4.1-4.5	60	49.7	50.3	37	91.4	8.6	21	80.0	20.0
4.6-5.0	77	25.7	74.3	20	23.4	76.6	69	68.3	13.7
5.1-5.5	55	43.9	56.1	23	15.1	84.9	45	57.3	42.7
5.6-6.0	35	36.6	63.4	9	11.8	88.2	30	40.0	60.0
6.1-6.5	23	38.2	61.8	0	—	—	17	36.4	63.6

[1]Apparent density of prey <150 μm = 2/mL.
[2]Apparent density of prey <150 μm = 0.1/mL.
[3]Apparent density of prey <150 μm = 1/mL.

fers <150 μm was equivalent to about 2 and 0.1/mL. In sum, the larvae switched to eating prey >150 μm on day 6 in the high-density rotifer treatment, day 7 in the low-density treatment, and day 8 in the copepod treatment (Table 7). If the analysis is based on larval size instead of larval age, selection for prey >150 μm occurs at 4.6-5.0 mm for northern anchovy fed the rotifer diets and at 5.6-6.0 mm for those fed the copepod diet (Table 7; Fig. 1).

Feeding intensity was highly variable on all diets. The observed stomach contents can differ by as much as a factor of three (Fig. 2) from the predicted stomach contents (C_{max}) used in the feeding models.

At high rotifer densities, northern anchovy filled their guts at a faster rate and consumed more. On average, fish eating the high-density rotifer diet were full within 2 hours, while those eating a low-density diet were full in about 3 hours. Comparing the average observed stomach contents, and excluding empty stomachs, for fish of equal age shows that all larvae eating at the high prey density ate more than their counterparts eating at lower prey densities (Table 8).

Growth

Hunter (1976) showed that the length-weight rela-

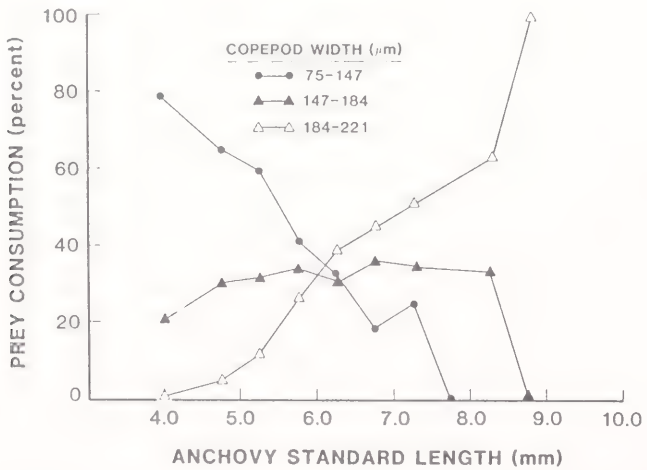

FIGURE 1.—Size of copepod prey eaten by northern anchovy related to fish size. See Table 1 for copepod width classes.

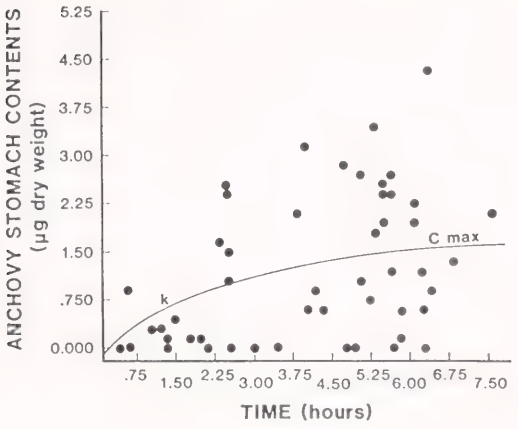

FIGURE 2.—Observed stomach contents of 4.0-4.5 mm northern anchovy fed 25 rotifers/mL, predicted rate of gut filling k and predicted maximum gut content C_{max}. Each point is one larva.

TABLE 8.—Mean dry weight of food (µg) observed in stomachs[1] of northern anchovy (n) related to their age.

Age (d)	Rotifers 25/mL		Rotifers 2/mL		Copepods 2/mL		Copepods 0.2/mL	
	n	µg	n	µg	n	µg	n	µg
5	9	1.75	17	0.60	8	0.18		
6	57	2.23	4	0.27	39	0.55		
7	8	3.56	5	1.41	37	0.67		
8	51	2.10	—	—	3	0.87	1	0.08
9	26	2.99	27	2.60	31	1.88	6	0.78
10	—	—	—	—			9	1.51
11	6	3.60	—	—			9	0.42
12	22	5.14	4	[2]6.39			3	0.90

[1]Average stomach contents (excludes empty stomachs) calculated for t = >3 hours; 3 hours is a reasonable time for northern anchovy to fill guts eating at lowest prey densities tested (see text).
[2]Day 13.

tion for northern anchovy was curvilinear on a log-log plot, and he used a Laird Gompertz model to describe both growth in length and in weight over 75 days. Because I am describing only the first 2 weeks of growth, I used a simpler exponential model (Table 4) which probably should not be used for larvae beyond 2 weeks of age.

Larvae grew at 0.35 mm/day on the copepod diet (k = 0.07) and at 0.33 and 0.25 mm/day on the high- (k = 0.06) and low-density (k = 0.05) rotifer diets (Table 4). On the average, the dry weight of larval northern anchovy was proportional to length to the third power. Depending on diet, the length exponent ranged from 2.80 to 3.16 (Table 4).

Daily percent increases in dry weight for northern anchovy fed the rotifer diets were 15% for larvae fed 2/mL and 21% for larvae fed 25/mL. However, northern anchovy grew the most, 23% per day, on the 2/mL copepod diet. For the three diets tested, daily growth in dry weight as a percent was constant over the size range.

An analysis of covariance was used to test for diet-induced differences in the relation between natural logarithms of length and weight for larval northern anchovy between days 5 and 9 when prey concentrations were controlled. Larvae which fed on copepods were significantly longer and heavier at age than larvae eating rotifers. There were no length or weight differences at age 7 days between the two rotifer treatments (Table 9), but there were differences in growth thereafter. Larvae raised on the two rotifer diets were the same weight at 4.9 mm (30.75 and 33.25 µg; P = 0.3), but larvae raised on copepods weighed less at 4.9 mm (28.54 µg) than larvae fed on the rotifer diets (P = 0.11 and <0.01).

I compared the distribution of my northern anchovy dry weights at length for the rotifer and

TABLE 9.—Effect of diet on northern anchovy standard length (SL) and dry weight (W).

Diet	Density per mL	No. cases[1]	Age = 7 days: $\bar{x}$ SL (mm)	$\bar{x}$ W (µg)	Probabilities = SL and = W: 1 vs. 2 SL/W	1 vs. 3 SL/W	2 vs. 3 SL/W
1-Rotifers	25	34	4.78	28.36	0.20/0.71	0.00/0.00	0.00/0.00
2-Rotifers	2	14	4.61	27.33			
3-Copepods	2	28	5.28	35.11			

			SL = 4.9 mm: $\bar{x}$ W (µg)	Probabilities: 1 vs. 2	1 vs. 3	2 vs. 3
1-Rotifers	25	34	30.75	0.30	0.11	0.00
2-Rotifers	2	14	33.25			
3-Copepods	2	28	28.54			

[1]Case numbers contain 2-12 larvae depending on number in group that were weighed.

copepod diets with those in a study by Hunter (1976) where northern anchovy were fed *Brachionus*, 50-100/mL, and copepods, *Tisbe* 0.01/mL, at 17°C and *Gymnodinium* was fed as the first food. The curves show that among experiments there appear to be diet-induced differences in weight at length (Fig. 3).

Metabolism

The caloric equivalent of metabolism for northern anchovy larvae ranging in age from first feeding to 25 days was determined using the relation between the metabolic rate and fresh dry weight (Model 2, Table 5) and by converting the oxygen uptake to calories using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). I assume the metabolic rate approximates "routine" metabolism.

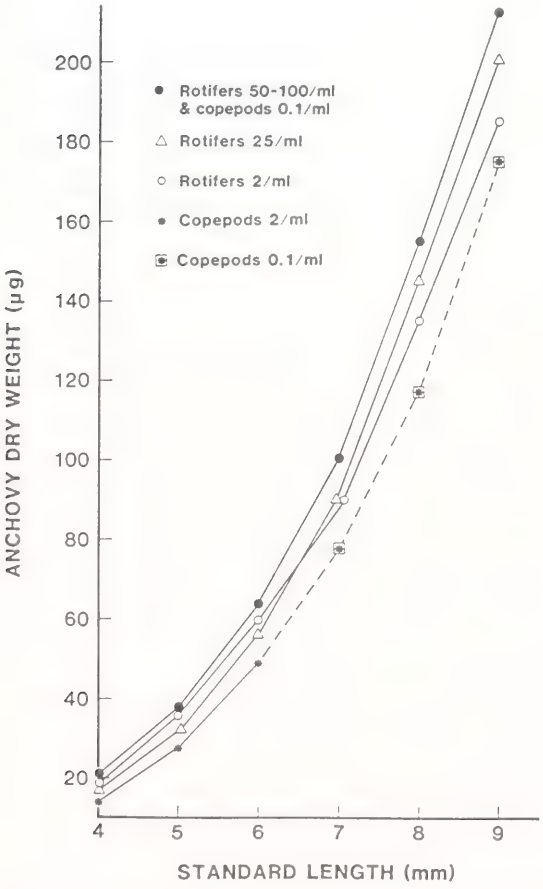

FIGURE 3.—Relation between dry weight and standard length for northern anchovy fed several diets where *Gymnodinium* was the first food.

I also determined the caloric equivalent of metabolism for first-feeding northern anchovy by starving them, determining the weight loss, and converting the loss to calories. Starving larvae lost an average of 10% of their body weight per day for 3 days, after which larvae must have continued to lose weight, but no decrease could be measured (Fig. 4). The time to maximum weight loss was 3-4 days, the time of irreversible starvation for northern anchovy from the onset of feeding (Lasker et al. 1970; Theilacker and Dorsey 1980). Larvae that weighed an average of 0.0211 mg at 3 days of age weighed an average of 0.0148 mg on day 6. The weight loss (0.0063 mg) $\times$ 5.4 cal/mg, which is the assumed caloric equivalent for northern anchovy tissue, equals 0.0339 calories, or a metabolic demand of 0.011 cal/day. This value, determined at a slightly lower temperature, corresponds well with the value obtained for first-feeding northern anchovy weighing 0.0211 mg using respiration measurements (0.013 cal/day).

Evacuation Rates

Gut clearance times for northern anchovy larvae appeared to be independent of larval age; however, the weight of food evacuated per hour increased with age because the stomach contents increased. Because the larvae fed at a constant rate after the gut was filled and defecated continuously, the gut clearance rate for actively feeding northern anchovy larvae was constant. The average gut clearance time for anchovy feeding on 25 rotifers/mL was 1.15 hours (SE = 0.13; range 0.7-1.5 hours; n = 6 tests). Reducing the prey density to 2/mL increased the average gut clearance time to 1.5 hours (range 1.2-1.8 hours; n = 2 tests) for the rotifer diet and 2.73 hours (SE = 0.26; range 2.0-3.3 hours; n = 4 tests) for the copepod diet.

Nonfeeding northern anchovy cleared their guts in 2.8-5.8 hours, depending on their size and stomach capacity (2.8 h/4.8 mm; 4 h/6.3 mm; 5 h/7.9 mm; 5.8 h/8.5 mm).

Daily Consumption of Rotifers and Growth Efficiency

Daily consumption was less on the low-density diet and, as a percent of body weight eaten per day, consumption ranged between 31 and 86%, depending on prey concentration and fish size (Tables 10, 11). For both rotifer diets, weight-specific consumption decreased with increasing body weight (Fig. 5).

Gross growth efficiencies were higher for north-

ern anchovy fed the low-density diet (Tables 10, 11). Mean gross-growth efficiency (days 5-14) based on dry weight was 0.30 for the high-density diet and 0.37 for the low-density diet. Based on calories, mean gross-growth efficiencies were 0.37 and 0.46 respectively.

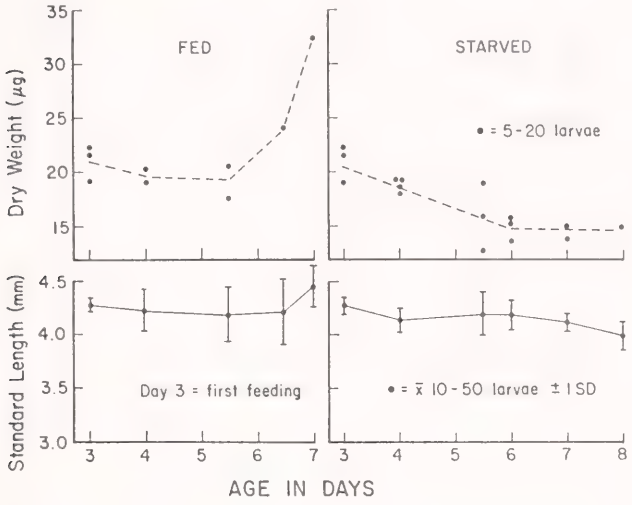

FIGURE 4.—Changes in standard length and weight of fed and starved northern anchovy larvae over time.

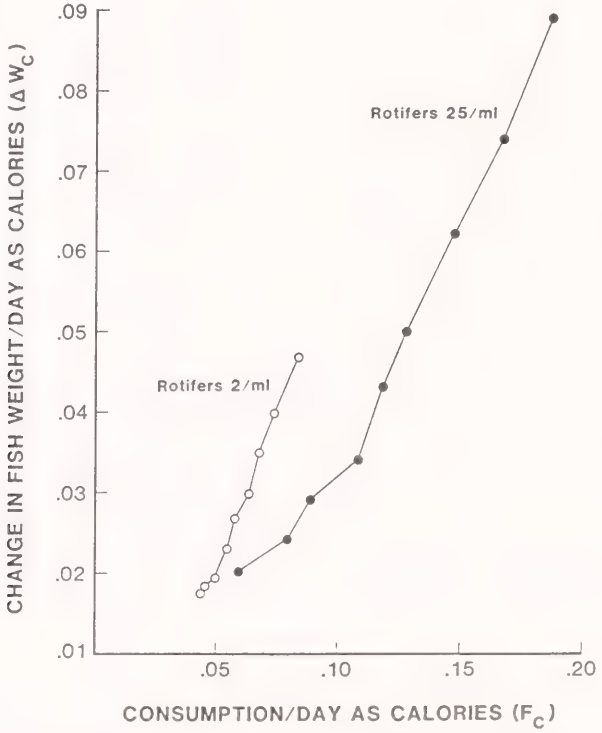

FIGURE 5.—Gross growth efficiencies (W_c/F_c; Tables 10, 11) of northern anchovy fed rotifers at 25/mL and at 2/mL.

TABLE 10.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 25/mL.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]
					Gut contents		Consumption					Change in fish weight				
Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Daily mean (μg)	Residual at end of feeding (μg)	Food (μg)	Body weight (%/d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	(cal/d)	(μg/d)	(cal/d)	Gross efficiency		Assimilation estimate
	A	l	W	r	$\bar{c}$	C_{12}	F_w	$F_{w/W}$	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
Rotifers (25/mL)	5	4.13	17.41	1.03	1.19	1.73	14.14	81	0.06	2.36	0.010	3.71	0.020	0.26	0.33	50.2
	6	4.39	21.12	1.34	1.54	2.00	18.11	86	0.08	2.77	0.012	4.38	0.024	0.24	0.30	44.4
	7	4.66	25.50	1.58	1.82	2.19	21.14	83	0.09	3.24	0.014	5.35	0.029	0.25	0.32	47.5
	8	4.95	30.86	1.80	2.07	2.39	23.99	78	0.11	3.80	0.016	6.31	0.034	0.26	0.31	45.7
	9	5.25	37.17	2.03	2.33	2.61	26.97	73	0.12	4.44	0.019	7.89	0.043	0.29	0.36	51.3
	10	5.58	45.06	2.28	2.62	2.88	30.23	67	0.13	5.21	0.022	9.27	0.050	0.31	0.38	55.6
	11	5.92	54.33	2.55	2.94	3.17	33.82	62	0.15	6.09	0.026	11.48	0.062	0.34	0.41	58.7
	12	6.29	65.80	2.88	3.31	3.53	38.04	58	0.17	7.14	0.031	13.77	0.074	0.36	0.44	61.7
	13	6.68	79.57	3.25	3.74	3.96	42.94	54	0.19	8.37	0.036	16.48	0.089	0.38	0.47	65.7
	14	7.09	96.05	3.68	4.24	4.45	48.67	51	0.21	9.79	0.042					

[1]Hatching = Day 0.

[2]$l_t = 3.06\, e^{0.061t}$; live length

[3]$W = 0.197\, l^{3.16}$ (on day consumption is estimated); fresh dry weight.

[4]$r = \bar{c}/1.15$ h (see text).

[5]$\bar{c} = \int_0^{12} C_{max}\,(1 - e^{-kt})/12 \cdot dt$.

[6]$C_{12} = C_{max}\,(1 - e^{-12k})$.

[7]$F_w = rt + C_{12}$; t = 12 h.

[8]$F_{w/W}$.

[9]$F_c = F_w \times 4.4$ cal/mg (see Table 1)

[10]μL O_2/d = 24 $(2.879\, W^{0.834})$ (see Table 5).

[11]Q_m 0.00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text)

[12]ΔW = weight gained 1 day after consumption estimated.

[13]$\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text).

[14]$\Delta W/F_w$.

[15]$\Delta W_c/F_c$.

[16]$P = \dfrac{Q_m + \Delta W_c}{F_c}$.

TABLE 11.—Estimation of growth efficiency of larval northern anchovy fed rotifers at 2/mL.

	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]	[12]	[13]	[14]	[15]	[16]
					Gut contents		Consumption									
Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Daily mean (μg)	Residual at end of feeding (μg)	Food (μg)	Body weight (%/d)	Calories (cal/d)	Metabolic rate (μL O_2/d)	(cal/d)	Change in fish weight (μg/d)	(cal/d)	Gross efficiency		Assimilation estimate
	A	l	W	r	$\bar{c}$	C_{12}	F_w	$F_{w/W}$	F_c		Q_m	ΔW	ΔW_c	$\Delta W/F_w$	$\Delta W_c/F_c$	P
Rotifers (2/mL)	5	4.03	18.77	0.72	1.08	1.23	9.87	53	0.043	2.50	0.012	2.87	0.015	0.29	0.35	67.3
	6	4.24	21.64	0.76	1.15	1.31	10.51	49	0.046	2.83	0.013	3.29	0.018	0.31	0.39	66.6
	7	4.46	24.93	0.83	1.24	1.41	11.33	45	0.050	3.18	0.015	3.60	0.019	0.32	0.38	68.4
	8	4.68	28.53	0.89	1.33	1.52	12.16	43	0.054	3.56	0.016	4.29	0.023	0.35	0.43	74.0
	9	4.92	32.82	0.96	1.44	1.64	13.16	40	0.058	4.00	0.019	5.09	0.027	0.39	0.47	79.3
	10	5.18	37.19	1.05	1.57	1.79	14.35	38	0.063	4.51	0.021	5.57	0.030	0.39	0.48	80.6
	11	5.44	43.48	1.14	1.71	1.94	15.62	36	0.069	5.06	0.023	6.56	0.035	0.42	0.51	85.5
	12	5.72	50.04	1.25	1.87	2.13	17.09	34	0.075	5.68	0.026	7.44	0.040	0.44	0.53	88.3
	13	6.01	57.48	1.37	2.06	2.34	18.82	33	0.083	6.38	0.030	8.69	0.047	0.46	0.57	92.2
	14	6.32	66.17	1.52	2.28	2.59	20.83	31	0.092	7.18	0.033					

[1]Hatching = Day 0

[2]$l_t = 3.14\ e^{0.05t}$; live length

[3]$W = 0.379\ l^{2.80}$ (on day consumption is estimated); fresh dry weight

[4]$r = \bar{c}/1.5$ h (see text)

[5]$\bar{c} = \int_0^{12} C_{max}\ (1 - e^{-rt})/12\ dt$

[6]$C_{12} = C_{max}\ (1 - e^{-12r})$

[7]$F_w = rt + C_{12}$; $t = 12$ h.

[8]$F_{w/W}$.

[9]$F_c = F_w \times 4.4$ cal/mg (see Table 1)

[10]μL O_2/d = 24 (2.879 $W^{0.834}$) (see Table 5)

[11]Q_m 0.00463 × μL O_2/d; (1 μL O_2 = 0.00463 cal) (see text)

[12]ΔW = weight gained 1 day after consumption estimated

[13]$\Delta W_c = \Delta W \times 5.4$ cal/mg (caloric estimation for larva) (see text)

[14]$\Delta W/F_w$.

[15]$\Delta W_c/F_c$.

[16]$P = \dfrac{Q_m + \Delta W_c}{F_c}$

DISCUSSION

Larval northern anchovy feeding ecology was similar to other larval fishes (Laurence 1977; Haegler and Outran 1978; Werner and Blaxter 1980; Theilacker and Dorsey 1980; Blaxter and Hunter 1982; Eldridge et al. 1982; Houde and Schekter 1981, 1983). As the larval northern anchovy grew they selected increasing larger prey, and on the rotifer diets, their feeding and growth rates increased with increasing concentrations of prey. In addition to the growth response to different prey concentrations, I observed differences in growth due to prey type. Fish grew the fastest on the copepod diet where one-third fewer calories were available than were available in the high-density rotifer diet ($4 \times 10\text{-}2$ vs. $13 \times 10\text{-}2$ cal/mL for prey <150 μm).

Length at age obtained for the first 2 weeks by larvae raised on copepods agreed with previous studies where northern anchovy were fed copepods and *Gymnodinium* was the first food (Kramer and Zweifel 1970; Hunter 1976). However, the larvae raised on copepods did not put on as much weight per unit length as their counterparts fed rotifers and *Gymnodinium*. Between days 5 and 9, the faster growing, copepod-fed larvae had significantly lower size-specific weights, and the weight exponents estimated for the first 2 weeks were lower, 2.9, than for larvae feeding on the high-density rotifer diet, 3.2. Lasker et al. (1970) found an exponent of 3.3 for northern anchovy fed on a high-density veliger and *Gymnodinium* diet.

These weight exponents estimated for northern anchovy are lower than the exponents of about 4 reported for deep-bodied fish larvae (haddock, flounder, cod, and scup; Laurence 1979). Likewise the exponents obtained for Atlantic herring ranged between 3.8 and 4.7 (reviewed by Checkley 1984). Weights of fishes used to estimate the exponents in the other laboratory studies ranged between 20 and 10,000 μg, whereas the northern anchovy weights ranged between 20 and 100 μg. Differences in growth rates occur as larval fish grow (Zweifel and Lasker 1976), and length-weight relations may change over the size range. Additionally, larval morphology is an obvious important component in the length-weight relation, and experimental variables may further complicate the relation. Moksness (1982) reported a low weight exponent of 2.6 for capelin, *Mallotus villosus*, from the field and from a large rearing basin. Both Atlantic herring and capelin larvae are similar in morphology to northern anchovy.

In previous laboratory feeding studies of larval northern anchovy, percent of body weight eaten per day was usually higher than consumption rates, 31-86%, I estimated. Reported values were 126-144% for northern anchovy (Hunter 1972), 197-440% for bigeye anchovy (Chitty 1981), and 20-295% for bay anchovy (Houde and Schekter 1981). Consumption varies with prey concentration and temperature, and the differences may be due to the experimental conditions. In the other studies, temperatures were higher and food concentrations were both lower and higher, with some including *Chlorella* blooms. However, it is likely that the differences are due to use of average food weights in the other studies. First-feeding northern anchovy larvae select small prey (Table 7; Fig. 1), and if average prey weight is larger than those actually being eaten by the larvae, their consumption may have been overestimated. For example, in Table 2, the average full stomach (C_{max}) of 4.25 mm fish (day 4-5) fed 25 rotifers/mL contained 15.55 rotifers while the average 4.75 mm fish (day 5-6) contained 7.79 rotifers. Using the width-specific weights (Table 1), I converted the 15 small rotifers to 1.8 μg and the 8 larger ones to 2.1 μg.

The exponent for the regression relating oxygen consumption to northern anchovy weight was 0.834 for larvae weighing <0.14 mg and 0.697 for larger larvae. Exponents have been reported for larval winter flounder, *Pseudopleuronectes americanus* (0.74; Laurence 1975); larval bay anchovy, *Anchoa mitchilli* (0.8; Houde and Schekter 1983); larval sea bream, *Archosargus rhomboidalis*, and larval lined sole, *Achirus lineatus* (0.838 and 0.942; Houde and Schekter 1983). Brett and Groves (1979) suggested a weight exponent of 0.86 for adult fish. There is considerable variation in respiration rates in the literature, probably depending on experimental conditions. The respiration rates given here for northern anchovy range between 3.1 and 6.9 μL/mg per hour for 0.02-2.7 mg larvae, and they are comparable to rates given for other fishes of similar age and size (reviewed by Theilacker and Dorsey 1980).

The evacuation rates determined here, 1.15-2.73 hours, for actively feeding northern anchovy larvae are comparable to rates of 1-3 hours estimated by Arthur (1976) for field samples. Particle residence time in the gut depended on prey density, prey type, and experimental design, e.g., feeding vs. nonfeeding larvae. Werner and Blaxter (1980) also showed that evacuation rates for herring fed *Artemia* were more rapid at higher prey densities, and because live and undigested prey were defecated, assimilation must have been low at these high prey densities.

Northern anchovy larvae, like herring, are con-

tinuous feeders, and at the high prey concentration, high consumption rates reduced the gut residence time and decreased digestion (assimilation; Tables 10, 11). At the lower prey concentration, the slower digestion time and increase in assimilation was not sufficient to compensate for the reduced consumption, and daily increase in weight, 15%, was less than the weight increase on the high-density diet, 21%. This result is similar to that in the recent study on assimilation by Pacific herring larvae fed *Brachionus* and *Artemia* (Boehlert and Yoklavich 1984). Using radioisotope tracers, Boehlert and Yoklavich found decreased assimilation at high food densities, but overall the larvae had a greater total energy gain at the high food densities because the higher food consumption more than compensated for the decreased assimilation.

Assimilation estimates, given here for northern anchovy larvae, fed two rotifer diets, averaged 53 and 79% and are somewhat higher than rates of 39-68%, depending on prey density, given by Boehlert and Yoklavich (1984) for Pacific herring. The assimilation estimates for northern anchovy larvae may not be reliable because the estimate assumes that weight-specific metabolic rates of fish fed both diets were equal. In addition, I made no attempt to correct for activity or to partition the portion of food assimilated into parts lost as feces and urine. Buckley and Dillman (1982) developed a technique to measure nitrogenous wastes of larval flounder. Assimilation efficiencies of 65-75% are commonly used in calculations of larval fish growth efficiencies (Ware 1975).

Estimates of gross growth efficiencies are not compromised by the above concerns. Larval northern anchovy gross-growth efficiencies increased with age, indicating that an increasing fraction of the calories consumed was translated into growth (Tables 10, 11). It is unrealistic that growth efficiencies would continue to increase. Brett and Groves (1979) suggested that for older fish growth rates become asymptotic with time. Growth efficiencies given here (24-46%) are consistent with growth efficiencies reported for other larval fish species (14-41% in Theilacker and Dorsey 1980) fed 1,000 or more prey per liter; reported efficiencies are high and extremely variable.

Direct observations of larval stomach contents showed that some rotifer-fed larvae fed at three times the average rate (C_{max}; Fig. 2). These fish may be the successful ones that survive in the field. Their high feeding rates would yield faster growth through the vulnerable larval stage. Feeding intensity also was highly variable for larvae eating copepods (Fig. 6), but the average number of copepods eaten was less than the average number of rotifers eaten (Table 2).

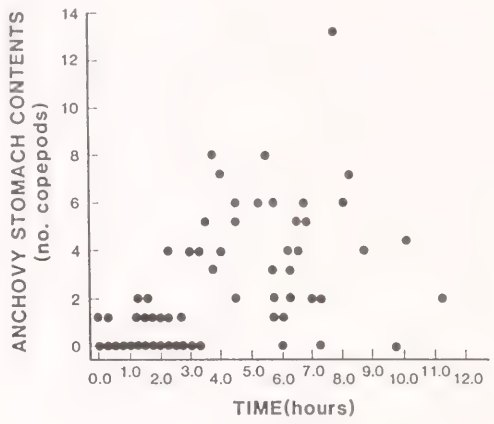

FIGURE 6.—Number of copepod nauplii observed in stomachs of 4.0-5.0 mm northern anchovy fed 2 copepods/mL. Each point is one larva.

Northern anchovy raised on copepods ate mainly *Gymnodinium*, augmenting their diet with copepod nauplii (Table 12). The stomachs of 96% of the 5-d-old larvae were full with *Gymnodinium* cells (Table 6). Fish were obtaining 60-90% of their daily caloric intake from *Gymnodinium*. This is evident by comparing the daily caloric intake (F_c) for day 5-6 larvae of equal size or weight that were fed copepods (Table 12) with those fed rotifers (Tables 10, 11). Consumption of 2-4 cells/minute can account for this energy input (4.2×10^{-5} cal/*Gymnodinium* cell [Vlymen 1977]), and successful feeding acts of this magnitude have been directly observed by Hunter (1981). Lasker and Zweifel (1978) developed a model (a modified version of Vlymen's [1977] model) to describe survival at sea in areas of various concentrations and proportions of large and small prey and concluded that large prey made very little contribution to survival of first-feeding larvae when sufficient (40 mL) small prey were available. As observed here, the ingestion of 10-20 copepod nauplii/day in addition to small *Gymnodinium* cells resulted in a growth rate of 0.35 mm/day, which is comparable to a rate of 0.37 mm/day reported for wild northern anchovy of similar age (Methot and Kramer 1979), and lends additional credence to Lasker and Zweifel's (1978) hypothesis that survival of northern anchovy depends on patchy (layered) distributions of small, abundant prey like *Gymnodinium*.

For all diets, an equivalent number of small prey,

TABLE 12.—Estimate of caloric input from copepods eaten by northern anchovy.

Diet	Age (d)	Standard length (mm)	Dry weight (μg)	Gut clearance rate (μg/h)	Gut contents Daily mean (μg)		Consumption		
							Copepods (μg)	Body weight (%/d)	Copepods (cal/d)
	A	*l*	*W*	*r*	$\bar{c}$ est	$\bar{c}$ obs	F_w	$F_{w/W}$	F_c
Copepods	5	4.34	20.35	0.07	0.19	0.16	1.07	05	0.0052
2/mL	6	4.66	24.99	0.10	0.28	0.30	1.55	06	0.0076
and	7	4.99	30.43	0.15	0.41	0.43	2.26	07	0.0111
Gymnodinium	8	5.36	37.39	0.23	0.62	0.68	3.44	09	0.0169
	9	5.75	45.77	0.35	0.96	1.08	5.32	12	0.0261

[1]Hatching = Day 0.
[2]$l_t = 3.06\ e^{0.07t}$
[3]$W = 0.297\ l^{2.88}$
[4]$r = \bar{c}$ est/2.73 h (see text).
[5]Estimated using equation in Table 3.
[6]Average stomach contents calculated for $t = >3$ h; includes empty stomachs.
[7]$F_w = 12\ r + \bar{c}$ est.
[8]% body weight eaten/d as copepods.
[9]Calories/d, copepods; $F_w \times 4.9$ cal/mg (Table 1).

Gymnodinium cells, was available and the concentration of large prey was varied. Availability of large prey of a suitable size in the copepod diet was 10 times the number available in the low-density rotifer diet. Because 4 mm (day 5) larvae fed copepods ate mainly *Gymnodinium*, and those fed the low-density rotifer diet ate mainly rotifers (Tables 2, 6), copepods nauplii must be more difficult to catch than rotifers, and consequently larvae consumed the more abundant *Gymnodinium* cells. Larvae which consume prey as they are encountered, rather than choosing a diet that maximizes the energy gained per unit foraging time, have been labelled "number maximizers" as opposed to "energy maximizer" in the parlance of Griffiths (1975) and Hughes (1979). Additional evidence that points to northern anchovy feeding as "number maximizers" is that, when prey of the proper size were available, their feeding rates paralleled prey abundance (Tables 10, 11).

The energy budget I calculated for northern anchovy fed rotifers at two concentrations gives information on their growth requirements that can be translated to growth requirements in the field. My data support Boehlert and Yoklavich's (1984) and Checkley's (1984) conclusions that larval fish may exhibit a high growth rate or a high growth efficiency, but not both at the same time. Boehlert and Yoklavich studied Pacific herring, which are 2-4 times the weight of northern anchovy, but like anchovy feed continuously, and found that as consumption increased, the total amount of food assimilated continued to increase despite a decrease in the efficiency of the assimilation. Checkley studied Atlantic herring and found that the gross growth efficiencies of Atlantic herring increased with increasing consumption, but he showed that the relation was peaked, and by incorporating results from the literature for other species, he also described a decrease in growth efficiency at high consumption for larval fishes.

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THIRTY-FOUR SPECIES OF CALIFORNIA ROCKFISHES: MATURITY AND SEASONALITY OF REPRODUCTION

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ABSTRACT

The viviparous rockfishes (*Sebastes* spp.) differ among species in age and size at maturity, and in the timing of peak spermatogenesis, fertilization, and larval extrusion. Age at 50% maturity ranges from 2 years in *S. jordani* to 9 years in *S. diploproa*. Within species, males usually mature either at the same age and size as females or at a younger age and smaller size. Rockfishes have two major seasons of larval extrusion, winter (November-March) or spring (April-July). The reproductive season for a particular species will fall within one of the major seasons throughout its geographic range. Within the major season, annual variations in the peak month of larval extrusion was observed for individual species. A long reproductive season and variations in the annual timing of that season are evidence of plasticity in the reproductive biology of rockfishes.

Reproductive development at the cellular level was compared with the coincident changes in the gross morphology of the gonads. The resulting description of the developmental sequences of the testes and ovaries enables the determination of maturity stage in the field.

Reproductive parameters such as age and size at maturity have been shown to be adaptive characteristics and are responsive to external pressures. For example, reduced population size due to fishing pressure may be associated with increased growth rate, reduced age at maturity, decreased fecundity, or a change in the gonadal index (Adams 1980; Gunderson 1980). For haddock, *Melanogrammus aeglefinis*, age at maturity was reduced and growth rates increased as the fishery increased (Templeman and Bishop 1979; Beacham 1983). Clupeoids shifted spawning location or time, and reduced age at maturity (Murphy 1977; Blaxter and Hunter 1982). A study of depleted populations of Pacific mackerel, *Scomber japonicus*, suggested a direct relationship between population size and age at maturity (Parrish and MacCall 1978). Pacific halibut, *Hippoglossus stenolepis*, stocks also showed reduced age at maturity and increased growth rates with reduced populations (Schmitt and Skud 1978). Age at maturity may thus be a useful indicator of heavy fishing mortality.

Rockfishes exhibit a variety of life history patterns, but only a few species have been studied in detail (Chen 1971; Miller and Geibel 1973; Patten 1973; Moulton 1977; Larson 1980; Love and Westphal 1981; McClure 1982). Previously, the most comprehensive work on the maturity of rockfishes was by Phillips (1964) and Westrheim (1975). Phillips (1964) sampled market landings from northern and central California over several years. For each of the 10 species he investigated, maturity was reported for the sexes combined, and ages at maturity were derived from back-calculated von Bertalanffy growth curves. Westrheim (1975) summarized 10 years of data gathered on trawl-caught fish off British Columbia and the Gulf of Alaska, for which he reported on size at maturity and reproductive seasonality. Most of the fish in his study are commercially important species for British Columbia and, except for three species, do not occur off California.

There are some difficulties in assessing maturity stages and reproductive seasonality in rockfishes. One problem is the use of external morphology of gonads to determine maturity stages. Some researchers have questioned the accuracy with which immature fish can be distinguished from resting, mature fish during the nonreproductive months (Gunderson et al. 1980; Rosenthal et al. 1982). Also, the potential reproductive season may be protracted and the peak time of reproduction may shift within this season, so that short-term studies may be misleading. Thus, reported variation in length and age at maturity between studies could be the result of uncertainty in maturity-stage determinations.

In this study, I clarify the determination of sexual maturity stages, determine age and size at sexual maturity, and survey the reproductive seasonality for 34 species of rockfishes from the waters off

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northern and central California, from Port San Luis to Crescent City. I outline the reproductive patterns among species and annual variation within species.

MATERIALS AND METHODS

Data for this study were collected between July 1977 and July 1982 from three sources: 1) a coastwide survey for adult rockfish made in July and August 1977 (Gunderson and Lenarz 1980); 2) an ongoing cooperative program, initiated in 1977 by the California Department of Fish and Game and the National Marine Fisheries Service, to sample the commercial (Sen 1984) and sport rockfish landings in northern and central California; and 3) a 1980 expansion of the cooperative program, to include data on gonad condition, prey items, seasonal fluctuation of interstitial fat, and gonad volumes. Additional collections were taken during cooperative survey trips with the National Marine Fisheries Service, Southwest Fisheries Center, and the California Department of Fish and Game. Fish were collected to supplement rarely sampled species and subadults that were not well represented in the three surveys.

Information on maturity was gathered primarily for seven species of commercial and sportfishing importance. Data for 27 additional species are presented, but these were inadequately sampled for statistical treatment of the data (Table 1). For each fish sampled from 1977 to 1982 the species, sex, and total length (mm) was determined in the field and otoliths were collected for age determination. The viscera from each of the 16,444 fish sampled from 1980 to 1982 were removed, preserved in 10% buffered formalin, and sent to the laboratory for analysis. In the laboratory the sex was verified and the maturity stage of the gonads was determined based on the criteria defined in this paper. Total length was measured from the most anterior part of the jaw to the dorsal tip of the caudal fin. When necessary, total lengths were converted to fork length to compare this study with others (Echeverria and Lenarz 1984).

Ages were determined for all fish investigated in this study. Most estimates of age were made from the surface of whole otoliths immersed in 70% ethyl alcohol, under a dissecting microscope at 12×. Standard techniques for counting annuli on whole otoliths were followed (Kimura et al. 1979; Shaw and Archibald 1981). Certain species such as *S. diploproa* required thin sectioning techniques for counting annuli (Beamish 1979). In some species it is difficult to determine what constitutes an annulus (Table 1), and consequently those ages have not been validated. The "break-and-burn" method of age determination (Chilton and Beamish 1982) is useful and more accurate than surface ages when aging fish older than 16 years (Tagart 1984). Ages were not redetermined in this study because the age at maturity occurs before 16 years. Maximum ages, however, may be underestimated.

The gonad conditions described for males are immature, maturing, mature (peak spermatogenesis), spent, and resting. For females, they are immature, maturing, mature (fertilized), ripe (eyed larvae), recently spent, and resting (Lyubimova 1965; Westrheim 1975; Gunderson et al. 1980). Histological sections were examined to define seasonal maturation and the sections were analyzed based on the criteria established by Moser (1967b) for *S. paucispinis* and by Lisovenko (1970) on *S. alutus* for mature fish. The development of germ cells into spermatozoa or mature oocytes was examined to determine the developmental sequence leading to maturity. Cellular development was compared with the external morphology (Westrheim 1975; Gunderson et al. 1980) to understand clearly the developmental sequence and to aid in the interpretation of maturity stages in the field. Gonads were subsampled from fish in all maturity stages. Whole gonads were sectioned and stained with hematoxylin. Histological sections were examined from 519 testes and 708 ovaries from 30 species (Table 1). Egg diameters were routinely measured from histological sections and checked against whole eggs using an ocular micrometer.

To determine age and size at maturity and reproductive seasonality, the approximate age and size when 50% and 100% of the males and females were mature were estimated for each species. For those commercial species for which large samples were available, I checked the accuracy of the rough maturity estimates by applying the method of Gunderson et al. (1980). These authors used the logistic model

$$P_x = \frac{1}{1 + e^{ax+b}}$$

where P_x = proportion mature at size x, and a and b are constants, to estimate the length at 50% maturity for a sample. I applied a transformation of this equation

$$\ln \frac{1}{P_x} - 1 = ax + b$$

to obtain estimates of a and b for size and age by

TABLE 1.—Sample characteristics used to determine age and size at maturity and seasonality for *Sebastes* from central California.

Species of *Sebastes* (common name)	Sampled		Total number		Histology	
	Age (yr)	Size (cm TL)	Immature (*N*)	Mature (*N*)	Males (*N*)	Females (*N*)
alutus (Pacific ocean perch)	5-16	26-54	2	83	2	2
auriculatus (brown rockfish)	1-19	10-52	140	281	16	20
aurora (aurora rockfish)	5-19	20-39	2	92	—	1
babcocki (redbanded rockfish)	3-24	23-66	23	137	1	2
carnatus (gopher rockfish)[1]	2-14	9-37	14	99	3	3
caurinus (copper rockfish)	3-20	19-57	49	276	17	14
chlorostictus (greenspotted rockfish)[2]	3-33	16-57	83	236	17	18
chrysomelas (black and yellow rockfish)[1]	1-12	9-38	19	189	—	—
constellatus (starry rockfish)[2]	2-15	12-44	58	152	6	4
crameri (darkblotched rockfish)	2-24	12-56	42	365	6	27
diploproa (splitnose rockfish)	3-27	13-40	44	266	1	3
elongatus (greenstriped rockfish)	2-21	13-31	33	215	16	12
entomelas (widow rockfish)[3]	3-31	26-58	182	2,285	25	28
flavidus (yellowtail rockfish)[3]	4-32	25-56	548	1,762	30	40
goodei (chilipepper)[3]	2-21	21-59	256	2,312	35	34
helvomaculatus (rosethorn rockfish)[1,2]	5-11	20-28	7	25	1	1
hopkinsi (squarespot rockfish)[1]	2-13	12-30	15	45	—	—
jordani (shortbelly rockfish)[1]	1-12	12-20	47	635	9	9
levis (cowcod)[1,2]	2-22	24-90	17	24	—	—
maliger (quillback rockfish)[1]	6-15	22-44	4	45	3	—
melanops (black rockfish)[3]	2-21	25-61	265	469	29	46
melanostomus (blackgill rockfish)	6-27	25-56	17	109	1	2
miniatus (vermilion rockfish)	5-30	30-67	12	96	7	2
mystinus (blue rockfish)[3]	2-23	21-49	263	1,297	16	48
nebulosus (china rockfish)[1]	1-17	8-44	13	56	4	3
ovalis (speckled rockfish)[1,2]	3-15	23-49	6	101	—	2
paucispinis (bocaccio rockfish)[3]	2-26	32-83	1,402	2,404	170	245
pinniger (canary rockfish)[3]	3-26	22-69	564	641	61	105
rosaceus (rosy rockfish)[2]	3-12	14-32	26	167	30	17
ruberrimus (yelloweye rockfish)[2]	3-30	25-69	46	86	8	6
rubrivinctus (flag rockfish)[1]	4-18	19-45	4	38	3	—
rufus (bank rockfish)[2]	2-24	19-54	25	137	—	—
saxicola (stripetail rockfish)	2-17	14-38	11	102	—	5
serranoides (olive rockfish)[1]	4-19	23-54	47	187	3	9

[1]Denotes species not sampled every month for determination of seasonality.
[2]Denotes difficult to interpret otoliths for age determination.
[3]Denotes species of major importance in the sport or commercial fisheries of California.

standard linear regression. These estimates of a and b were then used to calculate estimates of size or age (x) at 50% maturity ($P = 0.5$). This was done for all species with a sample of 10 specimens or more for each length or age. Where adequate data existed, P_{50} for a species was calculated by year and area to investigate possible yearly or geographic variation.

Reproductive stages for mature individuals were summarized by month, and the percentages of individuals at each reproductive stage were used to determine principal months of spermatogenesis (approximates mating), fertilization, and larval extrusion for each species. Seasonality was described only approximately for those species that were not present in all months sampled (Table 1).

Reproductive months for mature females were determined and the percentage containing eyed larvae was noted. Data from 1981 through 1985 were tabulated to compare annual variability in the

reproductive months and/or the principal month of parturition.

RESULTS

Moser (1967b) described the seasonal changes in gonads of mature *S. paucispinis* and should be consulted for details of morphology. In this study a general description of all maturity stages is included with emphasis on the immature gonad and the transitional stages, which are difficult to interpret. The transitional stages are 1) the determination of the first reproductive year, particularly in species with small maximum size; 2) the prespawned testis during spermatogenesis compared with the spawning and postspawned testis when spermatogenesis is completed and mating is in progress or just completed; 3) the unfertilized egg stage compared with the recently fertilized egg; and 4) the nonreproductive season, compared with the beginning of vitellogenesis or spermatogenesis when the gonads are beginning to mature. A comparison of external morphology with the histological sections indicates that the same sequence of spermatogenesis/vitellogenesis, mating, ovulation, fertilization, and larval extrusion is followed for each species in this study. There were not sufficient samples of all 31 species to discern what developmental variations might exist on the cellular level (Table 1).

Developmental Sequence of Ovaries

The germ cells in ovaries are clustered in oogonial nests, which are present throughout the year in varying numbers. The ovary of an immature rockfish (Gonad Stage 1) consists primarily of oogonial nests with oocytes <0.14 mm in diameter. The ovarian wall is translucent and thin (approximately 0.1 mm thick). Externally the ovary appears translucent with a tiny egg mass (Table 2).

Approaching the first year of maturity (Gonad Stage 2), the ovary is filled with oogonial nests, follicles begin to form around maturing oocytes, and the ovarian wall is translucent and thin. There is no evidence of the resorption and reorganization seen in spent ovaries. Externally the ovary appears pink through the thin wall, and eggs about 0.2 mm in diameter are visible.

As the reproductive season approaches (Gonad Stage 3) eggs are produced by the oogonial nests and vitellogenesis begins, resulting in eggs enlarging from 0.2 to 0.5 mm in diameter. Follicles form around the maturing eggs, a capillary network develops throughout the ovary, and the ovarian wall begins to thicken from 0.3 to 0.5 mm. Externally the ovary appears either white or yellow and firmly packed with eggs in grapelike clusters. The eggs expand during this stage, so that during maturation

TABLE 2.—Reproductive development at the cellular and external morphology level for ovaries of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Oogonial nests with oocytes <0.14 mm. Ovarian wall (OW) 0.1 mm thick.	Small and translucent to pink. Ovarian wall (OW) thin.
2. First year maturity	Oocytes <0.2 mm. No evidence of resorption.	Pink with visible eggs. No black pigmentation. OW thin.
3. Vitellogenesis	Mature oocytes 0.2-0.5 mm in diameter within follicles. OW 0.3-0.4 mm thick.	Yellow or white opaque eggs in grapelike clusters. OW thickening.
4. Fertilization	Oocytes 0.9 mm. Yolk globule disintegration, ovulation, fertilization.	Large clear eggs free in ovarian cavity, but enveloped by a network of capillaries.
5. Eyed larvae (parturition)	Larvae developed within chorion with eyes pigmented black or yellow.	Large, soft, gray. Ovary breaks easily, and is filled with eggs and fluid.
6. Spawned	Oocytes 0.08-0.64 mm in diameter. Resorption of blood vessels, atretic oocytes, and residual larvae. Collapsed egg cases. OW 0.5-1.0 mm thick.	Flaccid, reddish-purple, or grayish from residual larvae. OW thick and tough.
7. Resting	Resorption and reorganization. Proliferation of oogonial nests. OW 0.5-0.9 mm thick.	Firm, gray to pink. Tiny black dots indicate residual larvae, OW thick, tough, and loose from eggs.

the ovary swells in size. The eggs remain opaque, and held within a follicle.

Fertilized eggs (Gonad Stage 4) are about 0.9 mm in diameter and have shed their follicles, and the yolk globules have disintegrated. Externally the eggs appear translucent yellow or white and are no longer held in tight grapelike clusters. They are held within an elaborate capillary network, not totally free within the ovary, though they are no longer held within a follicle.

Development of the embryos continues for about a month (Moser 1967a) until they develop pigmented eyes (Gonad Stage 5) and become ready for release. The pigmented eyes are usually black except in *S. ruberrimus* where they are yellow. Externally the ovary is gray (from the pigmented eyes) and very fragile. It breaks easily when handled and usually some larvae are prematurely extruded when the adult is captured.

After normal release of the larvae (Gonad Stage 6), the ovary consists primarily of an elaborate vascular system, larvae that were not extruded, and a few eggs which failed to develop (atretic oocytes). Externally it appears very mushy and reddish gray, with an opaque and flaccid ovarian wall.

Resorption and reorganization of the ovary (Gonad Stage 7) occur until vitellogenesis begins (Gonad Stage 3) again. During the months of reorganization (Figs. 1-7) there is evidence of residual larvae, eggs, and capillaries being resorbed, and a proliferation of oogonial nests producing eggs for the next reproductive season. The ovarian wall is between 0.5 and 0.9 mm thick. Externally the ovary is compact and loosely encased by an opaque wall. During resorption the ovary changes from reddish brown to grayish brown. When vitellogenesis begins again (Gonad Stage 3) the ovary appears yellow or white. There are usually a few pigmented eyes being resorbed through Gonad Stage 3 from the previous year's brood.

The principal external characteristic of an immature ovary entering the first reproductive season is the wall, which is thin (0.1 mm) and translucent. There are also no residual pigmented eyes in the ovary. A spent and maturing ovary from a mature fish usually contains remnants of resorbed larvae (evidenced as black dots) encased by a thick, opaque ovarian wall (0.5 to 0.9 mm).

Developmental Sequence for Testes

It is often difficult to distinguish an immature from a resting testis in rockfish because the presence of sperm in the testis is not necessarily an indication of the fish's maturity. Understanding the developmental sequence of spermatogenesis can help to identify the reproductive stage any time of year (Table 3).

Histological examination shows that the immature testis (Gonad Stage 1) consists of germ cells, primary spermatogonia, and secondary spermatogonia which lend a whitish color at the periphery. Externally the testis is threadlike and translucent, often with a hint of white from the developing spermatogonia.

Spermatogenesis begins at the periphery of the testis and moves centripetally, filling the lumen, the efferent ducts, and finally the sperm duct. A male approaching the first year of maturity (Gonad Stage

TABLE 3.—Reproductive development at the cellular and external morphology level for testes of *Sebastes* species.

Gonad stage	Cellular morphology	External morphology
1. Immature	Germ cells, primary and secondary spermatogonia.	Small, threadlike; transparent to white at periphery.
2. First year maturity	Spermatozoan cysts throughout testis. No residual sperm in tubules or ducts.	Small, ribbonlike, and white. No evidence of sperm in central duct (translucent).
3. Spermatogenesis	Large spermatozoan cysts throughout testis with spermatozoa in lumen.	Milky white and swollen, sperm throughout testis in cross section.
4. Spawning	Sperm duct and lumen filled with spermatozoa. Spermatogenesis ceases at periphery.	Large, soft, white; sperm flows freely when cut. Center of testis white, periphery becoming translucent.
6. Recently spawned	Abundance of germ cells at periphery. Resorption of sperm by tubular boundary cells.	Center is white in cross section, with the periphery becoming firm and darker.
7. Resting	Reorganization of testis. Germ cells line spermatogenic tubules.	Firm, compact, and vaguely triangular. Color dark gray/brown.

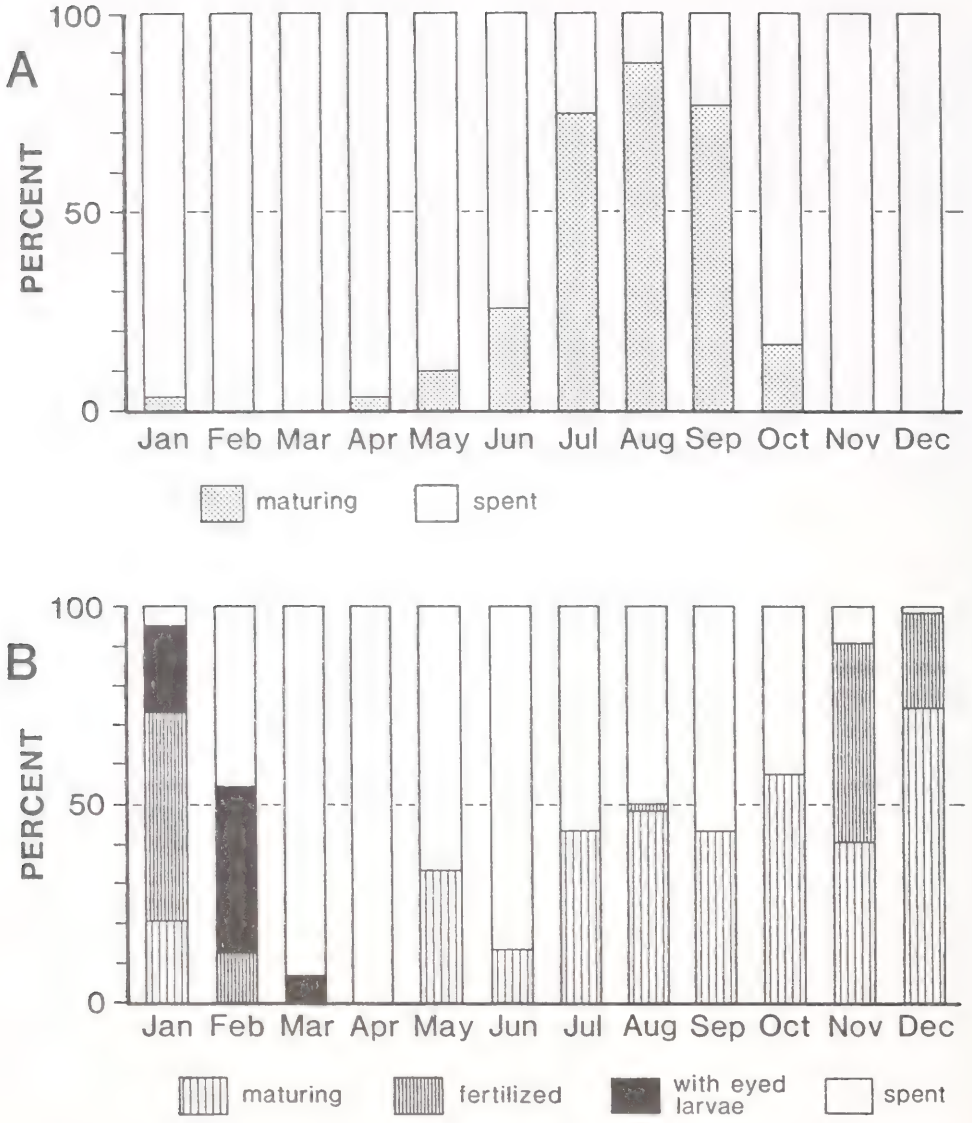

FIGURE 1.—A. Reproductive seasonality of mature males of *Sebastes entomelas* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. entomelas* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

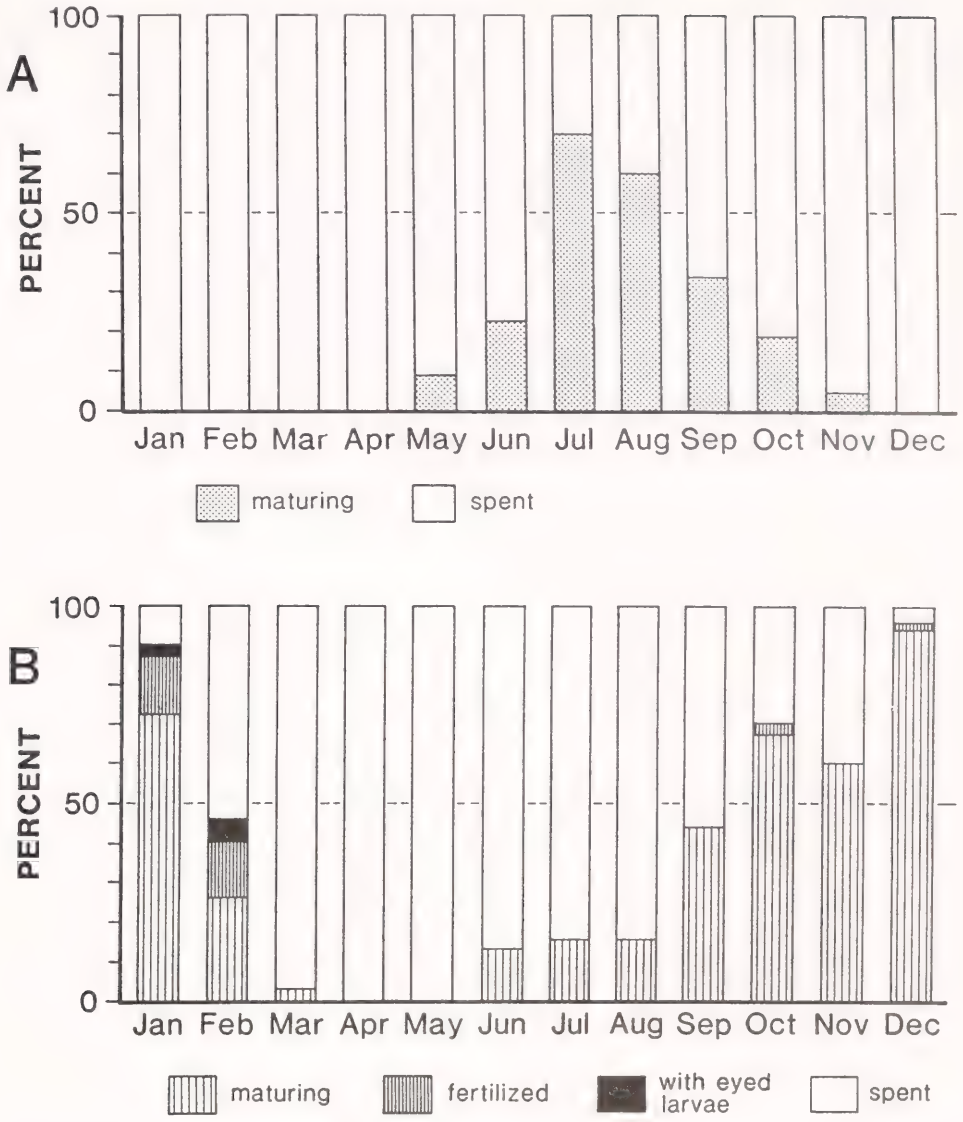

FIGURE 2.—A. Reproductive seasonality of mature males of *Sebastes flavidus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. flavidus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

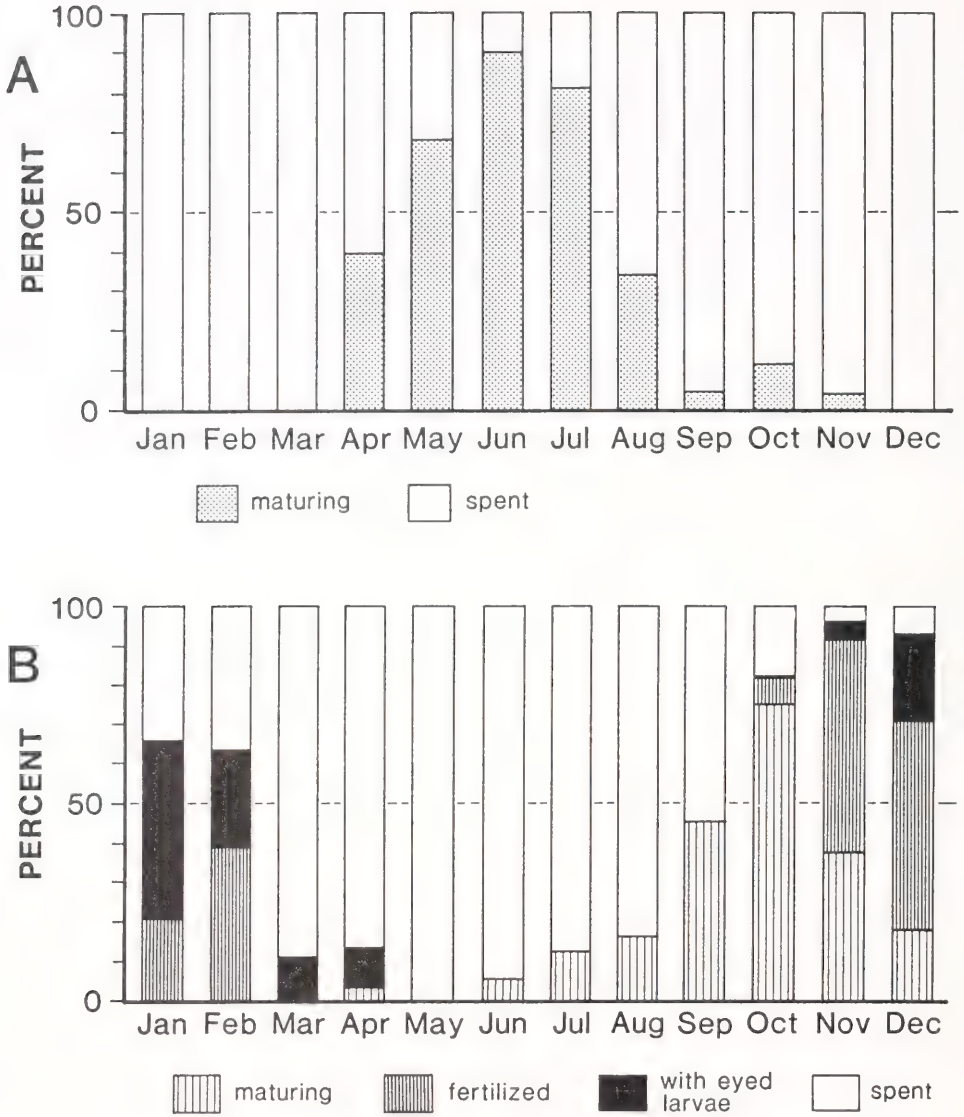

FIGURE 3.—A. Reproductive seasonality of mature males of *Sebastes goodei* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. goodei* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

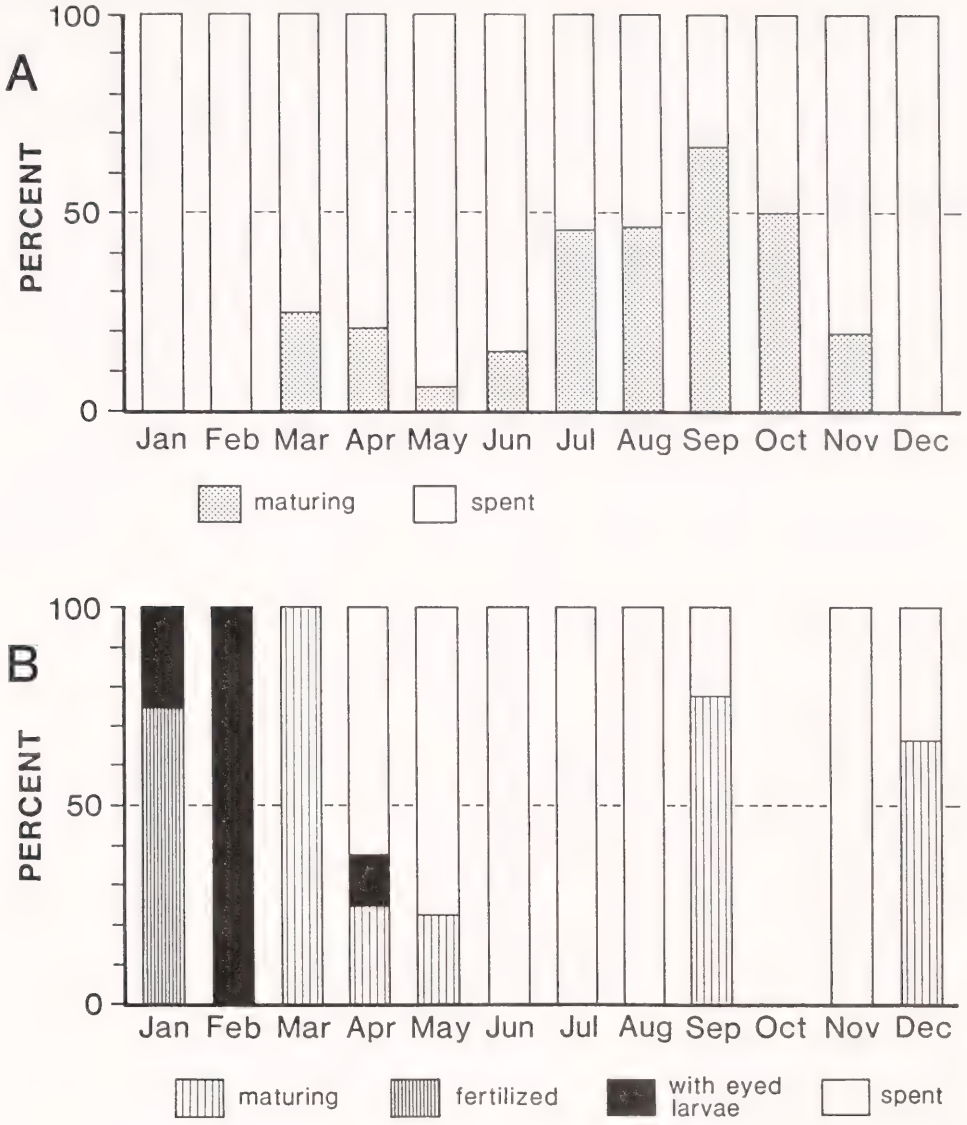

FIGURE 4.—A. Reproductive seasonality of mature males of *Sebastes melanops* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. melanops* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

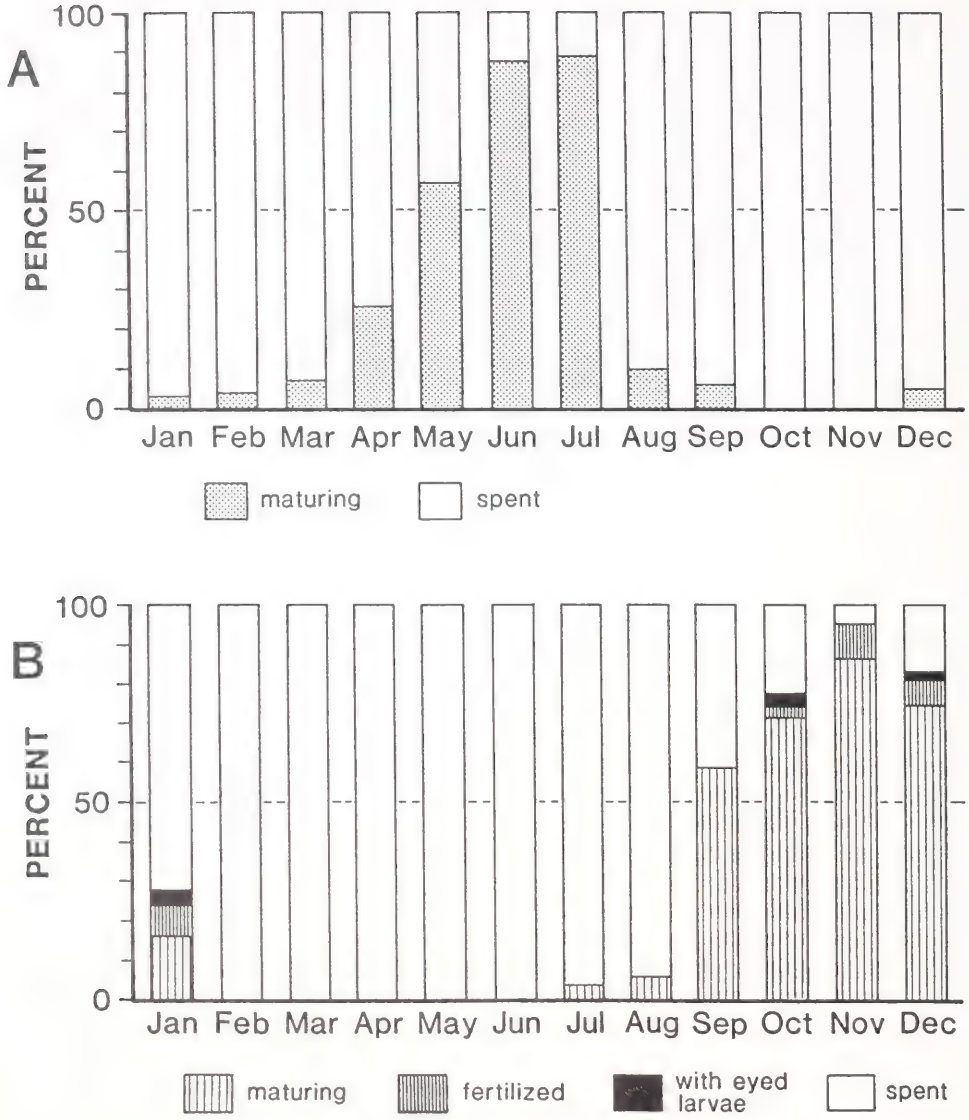

FIGURE 5.—A. Reproductive seasonality of mature males of *Sebastes mystinus* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. mystinus* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

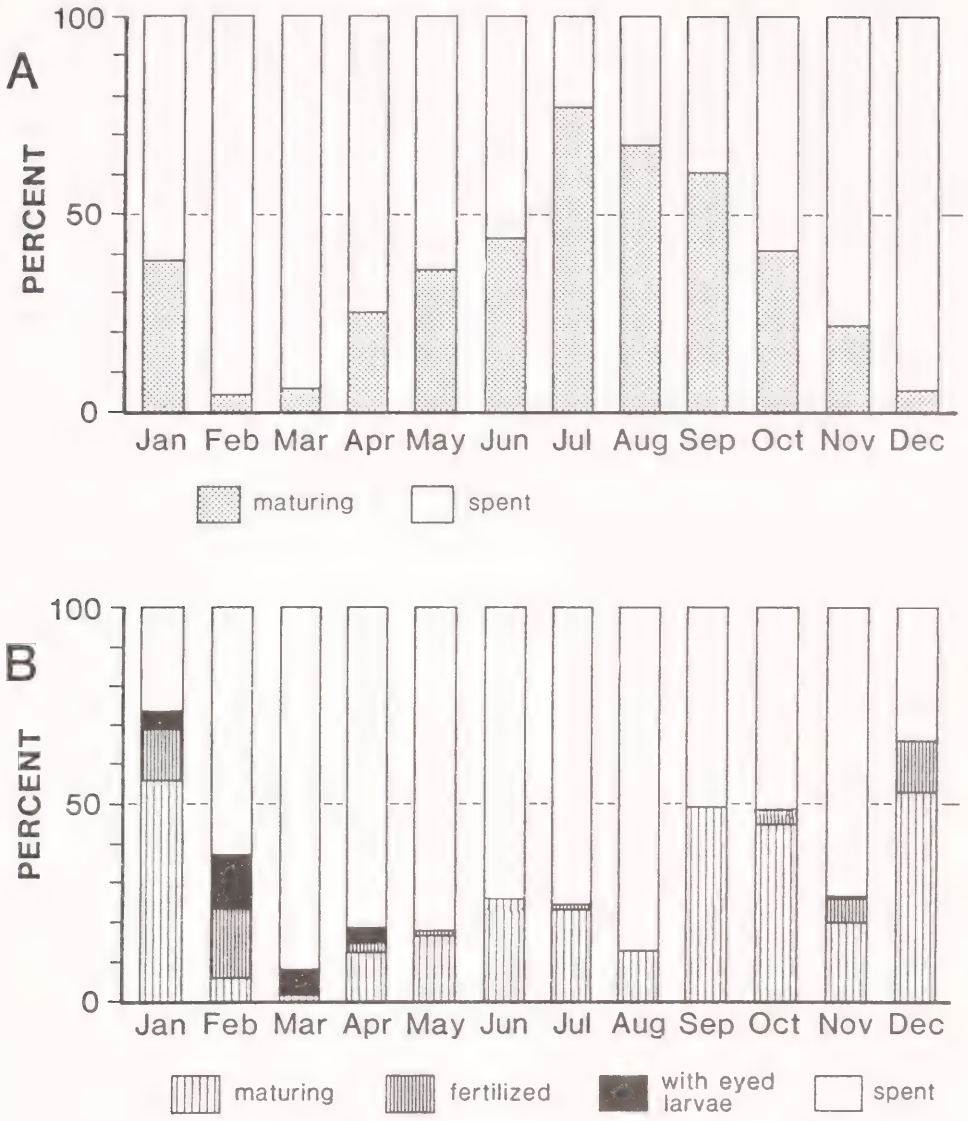

FIGURE 6.—A. Reproductive seasonality of mature males of *Sebastes paucispinis* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. paucipinis* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

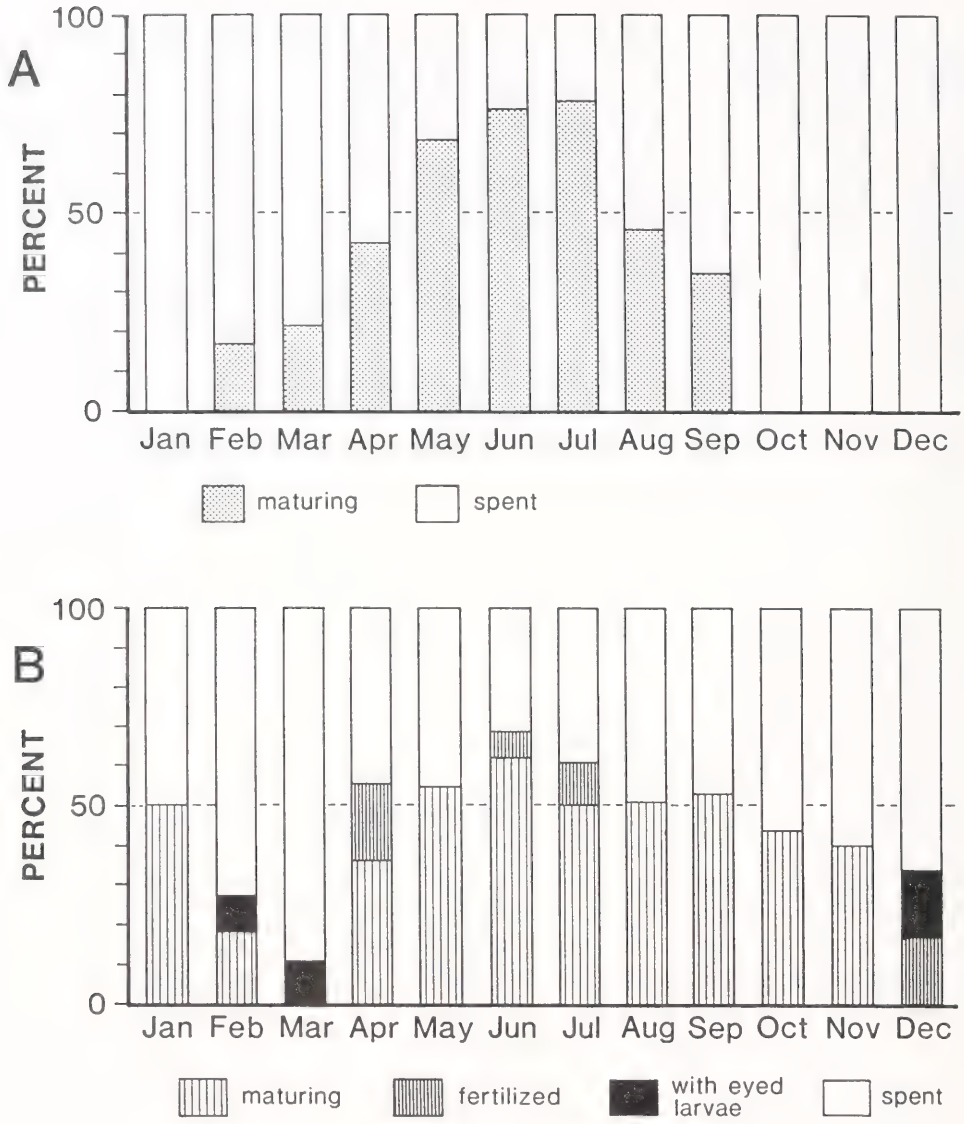

FIGURE 7.—A. Reproductive seasonality of mature males of *Sebastes pinniger* during 1980-82. Each bar shows the percent of mature males sampled that were maturing (Gonad stage 3 + 4) and spent (Gonad stage 6 + 7). See Table 2 for further definition of stages. B. Reproductive seasonality of mature females of *S. pinniger* during 1980-82. Each bar shows the percentage of mature females sampled that were maturing (Gonad stage 3), fertilized (Gonad stage 4), with eyed larvae (Gonad stage 5), and spent (Gonad stage 6 + 7). See Table 1 for further definition of stages.

2) has spermatogonial cysts developing throughout the testis. There is no sign of spermatozoa in the sperm duct. Externally, the testes appear slightly swollen and white; in cross section they are translucent in the center because of the absence of sperm in the sperm duct.

In a maturing male (Gonad Stage 3) spermatozoa appear throughout the testis in spermatozoan cysts. The sperm duct often contains remnants of residual sperm from the previous reproductive season. In a cross section the testis is swollen and whitish at the periphery and brownish off-white in the center because of the presence of residual sperm in the sperm duct.

As the reproductive season approaches (Gonad Stage 4) the spermatozoan cysts burst open, releasing spermatozoa into the efferent ducts and the sperm duct. Externally the testis is large, soft, and very white, sperm flows freely when the testis is pressed or cut. During the reproductive season spermatogenesis has ceased and the spermatozoa have moved from the periphery towards the sperm duct so that the periphery becomes hard and discolored. The central area may be swollen with sperm.

At the end of the reproductive season (Gonad Stage 7), the testis undergoes resorption and reorganization, wherein smooth muscle cells, connective tissue, and scattered residual spermatozoa, constituting cellular detritus, are evident in the histological sections. At the periphery, a new generation of germ cells reorganizes along the spermatogenic tubules. Externally the testis is a compact, irregular triangular shape that appears gray or brown.

An understanding of the developmental sequence on the cellular level aids in the interpretation of gonad stage in the field. The four, difficult to interpret, transitional stages can be clarified: 1) The first reproductive year is indicated by a white periphery (sperm) and an absence of sperm in the center of a cross section of testis, a thin ovarian wall and no residual pigmented eyes in ovaries. 2) The center of the prespawned testis is firm and a dark cream color (residual sperm); the periphery is white and swollen with sperm. The postspawned testis usually shows signs of white fluid (sperm) in the sperm duct and is firm and a dark cream color at the periphery. 3) Unfertilized eggs are opaque yellow or white held tightly in grapelike clusters while fertilized eggs are a translucent yellow or white and the outer eggs can be separated from each other. 4) Vitellogenesis is indicated by a deep yellow color and swelling of the eggs so that the ovarian wall fits tightly around the eggs; spermatogenesis is indicated by a softening and swelling of the testis and a whitening at the periphery.

Reproductive Maturity and Seasonality

Maturity was observed over a broad age and size range within species throughout the years sampled. The age and size at first maturity, 50% maturity and 100% maturity were estimated for males and females of each species (Table 4). Males reached 50% maturity either at the same or younger age than females. Size at 50% maturity is generally similar or somewhat smaller for males than for females of the same species. The standard linear regressions were run on the transformed logistic for the seven principal species occurring in this study, resulting in similar estimates of age at 50% maturity for *S. entomelas*, *S. flavidus*, *S. goodei*, *S. melanops*, *S. mystinus*, *S. paucispinis*, and *S. pinniger* (Table 5), and similar, if not exact, sizes at 50% maturity as estimates derived from the raw data. Maturity for species without sufficient data for statistical treatment are estimated from the raw data.

The reproductive season in *Sebastes* can be long with larval extrusion (parturition) seen in females of some species for up to 9 months (Table 6). From all the data collected between 1977 and 1984 a summary of principal month of spermatogenesis, fertilization, and parturition was determined for 32 species (Table 7). A span of 1 to 5 months between peak spermatogenesis and fertilization is seen. The time, when males ripen and mate, is not dependent upon the eggs being fully mature. The time between fertilization and parturition is usually about 1 month (Moser 1967a).

Reproductive seasonality for the principal species sampled is displayed graphically in Figures 1-7. Seasonality histograms are available, upon request, for most species investigated. The general trend in the seasonality of *Sebastes* is a prolonged reproductive period for each maturity stage. This trend is seen in the seven most abundant species sampled (Figs. 1-7). Spermatogenesis (Gonad Stage 3) occurs over 3 to 5 months before the testes are fully ripe (Gonad Stage 4). The timing of mating is estimated from the appearance of testes swollen with sperm. At least part of the male population is ready for mating for a period of 2 to 4 months. In females, generally, fertilized eggs (Gonad Stage 4) are found 1 to 3 months after mating. Eyed larvae (Gonad Stage 5) appear from 1 to 4 months after fertilized eggs were observed and were present in the sampled population for 3 to 6 months, usually with a

TABLE 4.—Estimated age and size at 1st, 50% and 100% maturity for given in cm

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
alutus	—	—	5	28	7	32	7	26	7	26	7	32
auriculatus	3	26	5	31	10	38	3	26	5	31	10	38
aurora	5	28	—	—	5	28	5	28	—	—	5	28
babcocki	3	27	4	31	5	36	3	32	4	34	6	41
carnatus	4	17	4	17	5	21	4	17	4	17	5	21
caurinus	3	30	4	32	7	40	5	31	6	34	8	41
chlorostictus	4	25	6	27	12	38	5	26	6	28	9	34
chrysomelas	3	14	3	16	5	20	3	14	3	15	5	19
constellatus	6	28	7	30	12	36	5	23	6	27	9	34
crameri	3	25	4	27	7	36	3	24	4	27	6	34
diploproa	7	20	9	22	10	29	6	18	7	19	9	23
elongatus	7	23	7	23	10	27	5	18	7	23	10	27
entomelas[1]	3	31	5	36	8	41	3	29	5	37	8	40
flavidus[1]	4	30	6	35	11	43	4	27	7	36	11	42
goodei[1]	2	26	3	31	7	38	2	29	3	34	6	39
helvomaculatus	7	22	7	22	10	27	5	20	8	23	10	27
hopkinsi	4	15	5	16	5	17	5	17	5	18	7	21

[1]Denotes samples from 1980-82 study only.

peak month of larval extrusion. The external appearance of individual ovaries indicates that larvae are in the eyed stage and ready for release throughout the ovary.

The total number of mature females observed during the reproductive months, and the percentage containing eyed larvae is presented for three commercially important species (Figs. 8-10). For the years 1981-85, variations in the months of parturition and/or the peak month is seen. *Sebastes entomelas* (Fig. 8) showed an annual variation in the months of parturition but not in the peak months (January-February). The peak month for *S. goodei* (Fig. 9) varied from December to February, and in *S. paucispinis* (Fig. 10) from December to March. A variation in which months larval extrusion occurs is seen in all three species. Chi-square tests showed the percentages to be dependent upon year and month. Therefore, there is a relationship between the percent-number of mature females with eyed larvae seen in a particular month, and reproductive year.

DISCUSSION

The reproductive biology of *Sebastes* follows the sequence of spermatogenesis, vitellogenesis, mating, ovulation, fertilization, and larval extrusion (Moser 1967b). As in other viviparous fishes (Turner 1947), sperm can apparently survive within the ovary for many months. In *S. mentella*, ovulation and the activation of sperm coincide with a change in pH (Sorokin 1967). The histological evaluation of the gonads in *Sebastes* of northern California confirms that spermatogenesis is generally completed and mating occurs before the completion of vitellogenesis. The length of time males are fully ripe can be up to 2 months in various species, and the delay between the time males are fully ripe and fertilization (sometimes up to 4 months) indicates that mating does not coincide with fully mature ova (Figs. 1-7). Testes are observed in decreasing degrees of ripeness after spermatogenesis has ceased. This indicates that one mating does not void the testes; males may mate more than once per season. Ovulation in teleosts is regulated by steroids and prostaglandins, which in turn are influenced to some degree by temperature, pheromones, or spatial/temporal cues (Stacey 1984). The presence of sperm in the ovaries of *Sebastes* does not trigger final oocyte maturation and ovulation; therefore, ovulation is probably influenced by environmental conditions. Thus knowing which conditions influence ovulation is necessary to determine some of the factors contributing to a successful reproductive year, as measured by the percent mature females with eyed larvae.

The costs of reproduction for females include the development of a highly vascular network throughout the ovaries, the nourishing of developing embryos (Boehlert and Yoklavich 1984), and the metabolism of waste products from the embryos (Moser 1967a). The ovaries must accommodate the added gonadal weight and volume until larval extrusion.

Sebastes from northern and central California collected 1977-82. Lengths total length (TL).

Species of *Sebastes*	Male						Female					
	1st		50%		100%		1st		50%		100%	
	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL	yr	TL
jordani	1	12	2	14	5	20	2	12	3	14	4	19
levis	4	32	4	32	4	32	4	32	4	32	5	37
maliger	4	22	4	22	7	31	6	26	6	26	7	28
melanops[1]	3	25	6	36	10	43	5	30	7	41	11	48
melanostomus	6	29	7	33	10	39	7	30	8	35	9	36
miniatus	5	35	5	38	8	43	5	37	5	37	9	46
mystinus[1]	4	22	5	27	9	32	5	22	6	29	11	35
nebulosus	3	26	4	27	6	30	3	26	4	27	6	30
ovalis	4	28	4	28	5	30	4	28	4	28	5	29
paucispinis[1]	3	32	3	42	7	55	3	36	4	48	8	60
pinniger[1]	4	28	7	40	9	45	4	27	9	44	13	54
rosaceus	4	16	6	20	8	25	4	15	6	20	8	25
ruberrimus	6	36	7	40	8	46	6	36	7	40	8	46
rubrivinctus	5	29	5	30	6	32	5	29	8	34	10	38
rufus	—	27	3	31	4	36	2	32	3	34	4	41
saxicola	3	15	3	16	4	17	2	17	2	17	3	18
serranoides	4	32	5	33	8	38	4	32	5	35	8	39

TABLE 5.—Standard linear regression used to estimate age (yr) and size (cm) at 50% maturity for males (M) and females (F) in seven species of *Sebastes*. Slope and *y*-intercept were estimated from the equation $\ln \frac{1}{P_x} - 1 = ax + b$. r = correlation coefficient, N = number of ages or sizes used in the regressions; each N represents at least 10 observations per age or size.

Species of *Sebastes*	Sex	Variable	*y*-intercept	Slope	50% maturity	*r*	*N*
entomelas	M	age	4.5598	−1.0006	5	−0.9588	6
		size	10.1042	−0.3162	33	−0.7649	11
	F	age	5.4800	−0.7982	5	−0.9647	5
		size	28.4810	−0.7810	37	−0.9667	4
flavidus	M	age	2.9748	−0.4994	6	−0.9577	10
		size	13.7834	−0.3964	35	−0.9718	14
	F	age	5.3731	−0.7757	7	−0.9541	9
		size	15.7482	−0.4331	36	−0.9723	13
goodei	M	age	1.1620	−0.4093	3	−0.9263	9
		size	7.7618	−0.3044	31	−0.8730	10
	F	age	3.7624	−1.1129	3	−0.9775	6
		size	12.2400	−0.3740	34	−0.9650	15
melanops	M	age	4.3841	−0.8011	6	−0.9769	6
		size	13.7147	−0.3814	36	−0.9411	6
	F	age	5.0627	−0.7149	7	−0.9760	8
		size	11.0749	−0.2720	41	−0.9520	16
mystinus	M	age	1.3482	−0.3669	5	−0.8530	10
		size	4.3885	−0.2049	27	−0.6778	11
	F	age	5.0097	−0.8022	6	−0.9680	9
		size	9.5090	−0.3368	29	−0.9218	17
paucispinis	M	age	1.7138	−0.6677	3	−0.9431	8
		size	10.7040	−0.2564	42	−0.9196	16
	F	age	3.5175	−0.8232	4	−0.9232	7
		size	13.7028	−0.2876	48	−0.9565	20
pinniger	M	age	3.7804	−0.5845	7	−0.9710	9
		size	11.2047	−0.2837	40	−0.9500	16
	F	age	5.1221	−0.5897	9	−0.9800	11
		size	11.5621	−0.5897	44	−0.9460	15

TABLE 6.—Months of parturition for species of *Sebastes* that occur in the northeastern Pacific Ocean. All available data are listed by area (results of this study in parentheses).

Species of *Sebastes*	Gulf of Alaska	British Columbia	Washington	Oregon	North-Central California	Southern California
aleutianus		Apr.[1]		May[2]		
alutus	May[3], Apr.-May[1]	Mar.[3]	Mar.[4]	Jan.-Apr.[2]	(Jan.-Mar.)	
auriculatus				June[5], May[6]	(Dec.-Jan.; May-July), May[7]	
aurora		>June[1]			(Mar.-May)	
babcocki		Apr.[1]		Apr.[2]	(May)	
borealis		Apr.[1]				
brevispinis		>May[1]				
carnatus					(Mar.-May), May[7]	
caurinus			Mar.[8], Apr.[6,9,5]		(Feb.)	
chlorostictus				Apr.[2]	(Apr.-Sept.)	Apr.-July[10], July[11]
chrysomelas					(Feb.-Mar.), Jan.-May[7]	
constellatus					(Apr.-May)	Mar. + May[10,11]
crameri	<June[1]	Feb.[1]		Feb.-Mar.[2]	(Nov.-Mar.), Nov.-Mar.[7]	
diploproa		July[1]	July[6]	Apr.-May[12]	(Jan.-Sept.), Feb.-July[13]	
elongatus		>June[1]		Apr.-May[12]	(May-July)	
ensifer						Feb. + May[10]
entomelas		Apr.[1]		Jan.[2,14]	(Dec.-Apr.), Nov.-Mar.[13]	
eos						Apr.-June[11]
flavidus		Mar.[1]	Jan.-Apr.[4]	Jan.-Mar.[2]	(Jan.-July), Nov.-Mar.[13]	
goodei					(Nov.-June), Nov.-Mar.[13]	Oct.-Mar.[11]
helvomaculatus	>May[1]	>May[1]			(May-June)	
hopkinsi					(Feb.-Mar.)	
jordani				Feb.[2]	(Feb.-Apr.), Nov.-Mar.[13]	
lentiginosus						Mar.[10]
levis					(Dec.-Feb.)	Dec.-Jan.[11]
maliger	May-July[15]	Apr.[1,16], May[5]			(Apr.-July)	
melanops		Jan.[17], <Apr.[1]		Jan.[17]	(Jan.-May)	
melanostomus					(Feb.-Apr.)	
miniatus					(Sept.) Nov.[11], Nov.-Mar.[13]	Nov.[11]
mystinus					(Nov.-Jan.), Nov.-Jan.[18], Jan.-Mar.[19]	
nebulosus					(Jan.-June), Jan.[20]	
nigrocinctus		May[1]				
ovalis					(May)	Jan.-May[11]
paucispinis		<Feb.[1]	Jan.-Apr.[4]	Jan.-Feb.[2]	(Jan.-May), Nov.-Mar.[11]	Oct.-Mar.[11]
pinniger		>Feb.[1]		Dec.-Apr.[2]	(Dec.-Mar.), Nov.-Mar.[11]	
proriger				Apr.-July[2]	(July-Aug.)	
reedi		May[1]		Feb.-May[15]		
rosaceus					(Apr.-July)	Mar. + May[10,11]
ruberrimus	June-Aug.[15]	May[1]	July[6]	Mar.-Apr.[2], Apr.-May[12]	(Apr.-June)	
rubrivinctus		May[1]		Apr.-May[12]	(July)	Mar.-June[10]
rufus					(Dec.-May)	
saxicola		Feb.[1]		Feb.[2]	(Jan.-Mar.), Nov.-Mar.[13]	
serranoides					(Jan.-Mar.)	Jan.[16]
simulator						Feb.-Mar.[10]
umbrosus						Apr.[10]
wilsoni		June[1]				
zacentrus	>May[1]	July[1]		Mar.-July[2], Apr.-May[12]	(May-June)	

[1]Westrheim 1975.
[2]W. H. Barss, Oregon Department of Fish and Wildlife, Marine Science Drive, Newport, OR 97365, pers. commun. 1985.
[3]Lyubimova 1965.
[4]Gunderson et al. 1980.
[5]Washington et al. 1978.
[6]DeLacy et al. 1964.
[7]Larson 1980.
[8]Patten 1973.
[9]Moulton 1977.
[10]Chen 1971.
[11]Moser 1967a.
[12]Hitz 1962.
[13]Phillips 1964.
[14]Barss and Echeverria 1987.
[15]Rosenthal et al. 1981.
[16]Love and Westphal 1981.
[17]Dunn and Hitz 1969.
[18]Wales 1952.
[19]Miller and Geibel 1973.
[20]Burge and Schultz 1973.

TABLE 7.—Reproductive seasonality for *Sebastes* from central California collected 1977-84. Listed by taxonomic order (Barsukov 1981).

Species of *Sebastes*	Principal month(s) of spermato-genesis	fertil-ization	parturi-tion
melanostomus	Nov.	Feb.	Feb.
aurora	Apr.	?	Apr.
ruberrimus	Dec.	Apr.	June
chrysomelas	?	Jan.	Feb.
carnatus	Dec.	?	Mar.
nebulosus	?	Jan.	Jan.
auriculatus	May	May	June
caurinus	Dec.	Jan.	Feb.
maliger	Dec.-Jan.	Apr.	Apr.
elongatus	?	Apr.	May
babcocki	Jan.	?	May
saxicola	?	Dec.	Jan.
diploproa	June	June	July
crameri	?	Dec.	Jan.
alutus	Sept.-Oct.	?	Mar.
pinniger	Oct.	Dec.	Dec.
miniatus	July	?	Sept.
levis	Sept.-Oct.	Oct.	Dec.
rosaceus	May	May	June
constellatus	Dec.	Feb.	Apr.
chlorostictus	Feb.	Apr.	May
goodei	Oct.	Dec.	Jan.
jordani	Nov.	Jan.	Feb.
paucispinis	Oct.	Dec.	Feb.
ovalis	Nov.	?	May
rufus	Nov.	Nov.	Feb.
hopkinsi	Dec.	Feb.	Mar.
entomelas	Oct.	Jan.	Feb.
mystinus	Aug.	Jan.	Jan.
melanops	Oct.	Jan.	Feb.
flavidus	Sept.	Jan.	Feb.
serranoides	Nov.	Jan.	Feb.

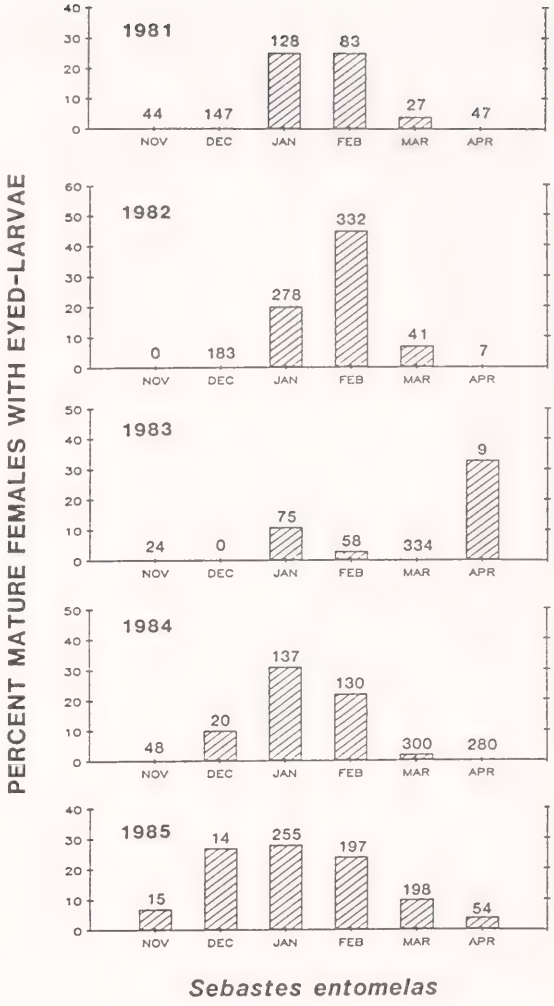

FIGURE 8.—Percent of mature female *Sebastes entomelas* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

Females are exposed to changing environmental factors from year to year, so flexibility in the timing of their greatest reproductive involvement may be advantageous. The apparent flexibility of the period between mating and larval extrusion may be a mechanism to optimize reproductive success. A long and variable period of larval extrusion is exhibited by the rockfish group (Figs. 8-10). The evidence of two spawnings per season have been reported for *S. paucispinis* (Moser 1967a), *S. ovalis*, and *S. constellatus* (MacGregor 1970). Multiple broods are indicated by the presence of eyed larvae undergoing resorption in the ovary concurrently with vitelloginic eggs at least 0.4 mm in diameter. During the years and throughout the area of this study, evidence of multiple broods was rare: only one *S. paucispinis* gonad showed evidence of a multiple brood. Moser's (1967b) detailed description of the histology of multiple broods indicates the development and extrusion of a second brood follows within 2 months of the first. In this study, two distinct seasons of larval extrusion, December and June, were noticed in *S. auriculatus* sampled from a limited area (Pt. Reyes-Half Moon Bay) (Table 6) in north-central California. The entire reproductive sequence in *Sebastes* seems to reflect a plasticity for reproduction that may enable the individual to respond adaptively to environmental factors.

The consequences of the reproductive biology in *Sebastes* include the absence of strong spawning pulses, the possibility of multiple mating of males, and flexibility in the timing of fertilization. Apparently mating is not restricted to a short period

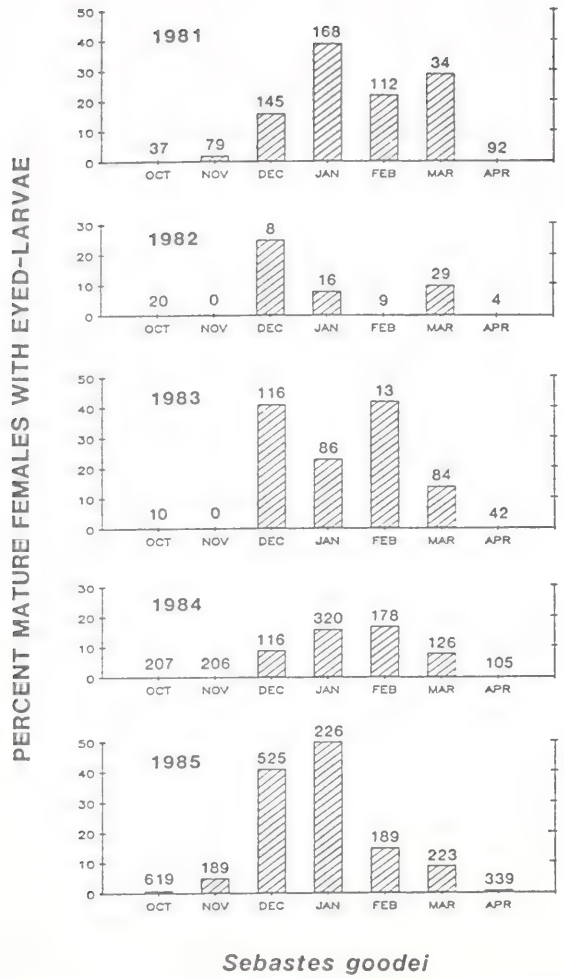

FIGURE 9.—Percent of mature female *Sebastes goodei* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

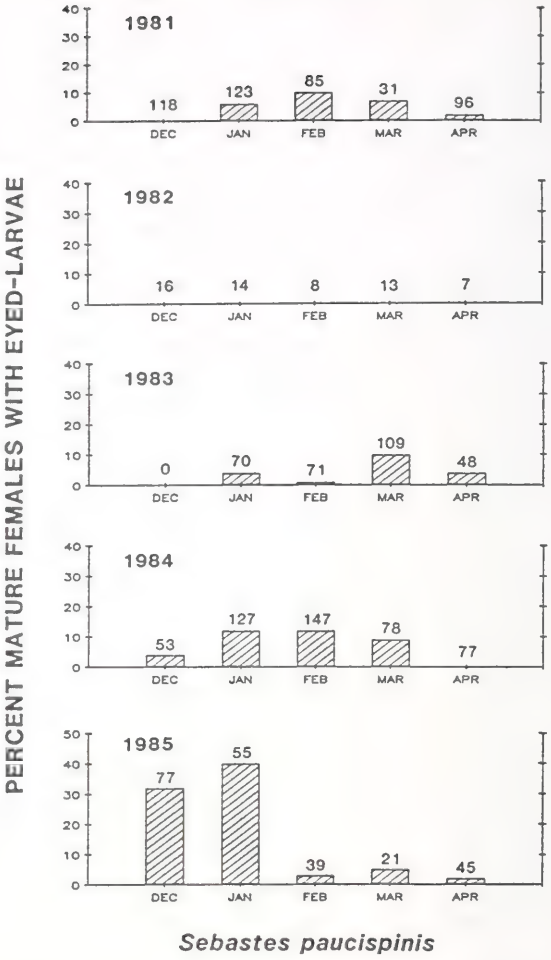

FIGURE 10.—Percent of mature female *Sebastes paucispinis* containing eyed larvae for the reproductive months during 1981-85. Total number of mature females observed are indicated over bars.

of time and elaborate displays to induce ovulation are not necessary. It is not surprising, therefore, to find so little information regarding mating behavior in the most speciose and populous group of fishes in north-central California (Helvey 1982).

Ages and sizes at maturity from this study generally agree with findings in the literature, but sometimes exhibit large discrepancies (Table 8). The variability has possible sources: differences in age determination techniques, length measurements, identification of the immature gonad stage, or sampling at times of the year when it is difficult to distinguish immature from resting fish. Previous studies on maturity often focused on adult populations or were based on samples taken only during summer, when most species are not in reproductive condition (Westrheim 1975; Gunderson et al. 1980; Rosenthal et al. 1981, 1982). The differentiation of an immature gonad stage versus mature "resting" gonads is most difficult and subject to error during the nonreproductive months.

Age and size at 50% maturity by area and year were calculated for *S. flavidus*, *S. goodei*, and *S. paucispinis* (Table 9). Age and size at maturity did not differ geographically but did vary between years. Age varies up to 1 year and size varies up to 3 cm. Apparently, there is some variability in age and size at maturity within a population between years. The normal range of variation of size and age

TABLE 8.—Age and size at 50% maturity for male (M) and female (F) *Sebastes* by area. All lengths are converted to fork length for comparison (Echeverria and Lenarz 1984).

Species of *Sebastes*		Alaska	British Columbia	Washington	Oregon	California	this study
auriculatus							
	M			4 yr, 23 cm FL[1]			5 yr, 31 cm FL
	F			4 yr, 25 cm FL			5 yr, 31 cm FL
entomelas							
	M		37 cm FL[2]		4 yr, 33 cm FL[3]	4 yr, 29 cm FL[4]	5 yr, 32 cm FL
	F		38 cm FL		7 yr, 38 cm FL		5 yr, 36 cm FL
flavidus							
	M	11-15 yr[5]	40 cm FL, 40.5 cm FL[2,6]			5 yr, 31 cm FL[4]	6 yr, 32 cm FL
	F	41-45 cm FL	42 cm FL, 45 cm FL				7 yr, 33 cm FL
goodei							
	M				26 cm FL[6]	4 yr, 28 cm FL[4]	3 yr, 29 cm FL
	F				37 cm FL	4 yr, 30 cm FL	3 yr, 32 cm FL
melanops							
	M	10-13 yr, 40-42 cm FL[5]		3 yr, 21 cm FL[7]	5 yr[8]		6 yr, 35 cm FL
	F	9-12 yr, 39-42 cm FL		3-4 yr, 33 cm FL	6 yr		7 yr, 40 cm FL
mystinus							
	M				3 yr[8]	6-7 yr[9]	5 yr, 26 cm FL
	F				4 yr	6 yr	6 yr, 28 cm FL
paucispinis							
	M		<57 cm FL[2]	5 yr, 45 cmFL[7]		4 yr[4]	3 yr, 39 cm FL
	F		<62 cm FL	6 yr, 48 cm FL		37 cm FL	4 yr, 45 cm FL
pinniger							
	M		41 cm FL[2,6]		12 yr, 39 cm FL[8]	5-6 yr[4]	7 yr, 39 cm FL
	F		48 cm FL		10 yr, 43 cm FL	33 cm FL	9 yr, 43 cm FL

[1]Washington et al. 1978; [2]Westrheim 1975; [3]Barss and Echeverria 1987; [4]Phillips 1964; [5]Rosenthal et al. 1982; [6]Gunderson et al. 1980; [7]Barker 1979; [8]McClure 1982; [9]Miller et al. 1967.

at maturity should be determined before subtle shifts in these parameters are studied.

Later spawning in high latitude populations occurs in some teleosts as a response to temperature and photoperiod (Wootton 1984). The existence of geographical trends for spawning months can be determined for a species if data exist for the same months and years. Parturition occurred somewhat earlier in the southern end of the range of *S. maliger*, *S. ruberrimus*, and *S. entomelas*. *Sebastes maliger* extruded larvae between May and July off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes ruberrimus* extruded larvae between June and August off Alaska (Rosenthal et al. 1981, 1982) and between April and July off California during 1982. *Sebastes entomelas* extruded larvae in February off Oregon and in January off California in 1982 (Barss and Echeverria 1987) (Table 6). For species where comparable data exist, parturition is earlier in the southern end of the species range.

TABLE 9.—Age and size of three *Sebastes* species at 50% maturity derived from linear regressions for males (M) and females (F) by area and by year for the area between Crescent City and Morro Bay.

		S. flavidus		*S. goodei*		*S. paucispinis*	
Data base	Sex	yr	cm TL	yr	cm TL	yr	cm TL
North of Point Arena	M	—	—	4	—	3	43
	F	—	—	4	—	4	48
South of Point Arena	M	—	—	4	31	3	43
	F	—	—	4	33	4	47
April 1980-March 1981	M	6	35	4	31	3	43
	F	7	37	4	34	4	48
April 1981-March 1982	M	7	38	5	33	3	42
	F	6	36	4	32	4	47
April 1980-Mach 1982	M	6	35	4	31	3	43
	F	7	36	4	34	4	48

Reproductive seasonality can be classified into one of two broad seasons, early (winter) or late (spring-summer) (Phillips 1964), which seems to hold true throughout a species range (Table 6). The duration of larval extrusion varies from 1 to 9 months and is species-specific. Closely related species have similar seasons of parturition, but the peak month may differ (Table 7).

Data on parturition may be useful when investigating recruitment by estimating annual reproductive success. To predict year-class strength for species of *Sebastes*, it must be possible to identify species in the juvenile stages. Juvenile identifications have been described for 18 species of rockfish

that occur off California (Moser and Ahlstrom 1978; Richardson and Laroche 1979; Laroche and Richardson 1980, 1981; Anderson 1983); the difficulties of differentiating between similar species are evident in these studies. Knowledge of the principal month of parturition may be a useful tool when identifying species in the age 0 population. Principal month of parturition would have to be documented for the year that recruitment is investigated.

Life history parameters that are interrelated, such as growth, maturity, and fecundity, can be influenced by external conditions, such as temperature, prey abundance, and predation (Stearns and Crandall 1984). The manner in which they can be affected is species-specific and may change in a predictable manner. Observed changes that coincide with reduced population sizes include increase in growth rates (Templeman and Bishop 1979), decrease in age at maturity (Murphy 1977; Parrish and MacCall 1978; Schmitt and Skud 1978; Templeman and Bishop 1979), and decrease in size at maturity (Alm 1959; Pitt 1975). Stearns and Crandall (1984) proposed that changes in age and/or size at maturity are determined by genetic as well as environmental factors, so that populations will respond in a predictable manner. A shift in either the age or size at maturity in *Sebastes* may be an indication of a change in population densities. In order to detect any population changes, age and size at maturity for species should be determined yearly and within a well-defined geographic area. Fish of the estimated age and size at first maturity should be included—sampling from market fish tends to yield only mature fish. Ages should be determined from the same fish that are sampled for maturity.

Fecundity in poikilotherms is generally related to size; changes in growth rates and size at maturity will affect fecundity. Fecundity often relates more to body size in short-lived species and to available energy in long-lived species (Ware 1980). Fecundity increases with size in at least some species of *Sebastes* (Phillips 1964), but annual reproductive success may be linked to available energy. Gonad volumes of female *S. flavidus* were reported for 1981 (Guillemot et al. 1985) and compared with volumes measured during the El Niño winter of 1983-84 (Lenarz and Wyllie Echeverria 1986); this comparison showed reduced gonad volumes in *S. flavidus* for the 1983 reproductive season. Whether the decreased gonad volume was due to egg size or number was not determined.

Shifts in age and/or size at maturity may occur in species that have a multigenerational, late-maturing population. In his studies of flatfish populations, Roff (1982) predicted that size at maturity would be primarily influenced by size-dependent mortality and that changes in size at maturity would occur in species where growth to a minimal size is more adaptive than early reproduction. Changes in age at maturity will more likely occur in species that mature early. Changes in size, rather than age, at maturity would most likely occur in *Sebastes* subjected to overfishing or long-term environmental stress.

General changes in life history parameters may be predictable according to a species' position on the *r-K* selection continuum. Increased fishing mortality resulting in decreased populations may affect life history parameters by increasing growth rates, reducing age at first maturity, increasing fecundity at age (Adams 1980; Gunderson 1980), and reducing variability in the gene pool by reducing the number of spawning groups in the more *K*-selected species (Leaman and Beamish 1984). The reproductive strategy of *Sebastes* reflects more *K*-type characteristics, which include later maturity, slower growth rates, lower individual fecundity, or some degree of parental care (Garrod and Horwood 1984). The *K*-type reproductive strategy enables a species to minimize the effects of a poor reproductive year (Roff 1984). A disadvantage for a heavily fished *K*-type species is the late age at maturity, as exists in *Sebastes*, so that the advantage of many reproductive seasons must be balanced against adult population size to obtain an allowable harvest.

The reproductive strategy of *Sebastes*, with multiple generations reproducing simultaneously and the plasticity of annual timing, results in a buffered system. The populations of exploited stocks of *Sebastes* should be able to recover from a single year of high mortality due either to poor recruitment or to adult mortality. However, overfished populations or long periods of poor recruitment could result in a reduced size at maturity and a corresponding reduced fecundity.

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DISTRIBUTION, ABUNDANCE, REPRODUCTION, FOOD HABITS, AGE, AND GROWTH OF ROUND SCAD, *DECAPTERUS PUNCTATUS*, IN THE SOUTH ATLANTIC BIGHT[1]

L. STANTON HALES, JR.[2]

ABSTRACT

Five years of bottom trawling indicated that round scad were abundant and widely distributed throughout the South Atlantic Bight in summer and fall, but less abundant and restricted to deeper (28-110 m), warmer (>15°C) waters in winter and spring. Adults and juveniles were spatially segregated, with adults dominating catches in inner and outer shelf regions and juveniles dominating midshelf regions year round. Catches over sponge-coral habitat were significantly greater than catches over sand bottom in winter, whereas catches over the two bottom types were similar in other seasons. This seasonal change in distribution may relate to higher productivity and temperature stability of live bottom habitats. Stomach contents indicated that round scad are diurnally feeding zooplanktivores; diets changed seasonally and increased in prey diversity with growth. Round scad spawn repeatedly from March through September. Daily growth analysis revealed that both sexes mature in 4-5 months at approximately 11 cm fork length. The life span of round scad could not be determined because the growth record of otoliths of most adults was irregular.

Fishes of the genus *Decapterus* occur in most neritic and some oceanic waters of tropical, subtropical, and temperate latitudes. Little is known of the biology of most species, except for those species which support fisheries in the Hawaiian Islands, the Philippines, Japan, and the west coast of Africa (Yamaguchi 1953; Tiews et al. 1970; Akaoka 1971; Boely et al. 1973). Although the taxonomy of Indo-Pacific species is unclear (Berry 1968), three species are recognized in the western North Atlantic: the redtail scad, *Decapterus tabl* Berry; the mackerel scad, *D. macarellus* (Cuvier); and the round scad, *D. punctatus* (Agassiz).

The round scad occurs in the western Atlantic from Nova Scotia to Rio de Janeiro, Brazil, and throughout the West Indies and Bermuda (Berry 1968); however, little information is available concerning its basic biology. The distribution of the species has been determined from purse seine catches in the Gulf of Mexico (Klima 1971), where it supports a bait fishery, and from bottom trawl catches over sand bottom habitat in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980). The location and duration of the spawning season has been ascertained from ichthyoplankton surveys in the eastern Gulf of Mexico (Aprieto 1974; Leak 1981). In addition, Leak (1981) determined larval mortality and production, and estimated biomass and potential yield of round scad in the eastern Gulf of Mexico. The objectives of this study were to provide information on seasonal distributions, relative abundance, reproduction, feeding habits, age, and growth of round scad in the South Atlantic Bight.

METHODS

Seasonal Distribution and Relative Abundance

A stratified random sampling design (Grosslein 1969) was used to assign trawling stations within six depth zones (9-18 m, 19-27 m, 28-55 m, 56-110 m, 111-183 m, 184-366 m) on nine seasonal cruises (Table 1). A total of 739 stations were completed on the continental shelf and upper continental slope between Cape Fear, NC and Cape Canaveral, FL. Fishes were captured in a 3/4 scale version of a "Yankee No. 36" otter trawl (Wilk and Silverman 1976) with a 11.9 m headrope, a 16.5 m footrope, and a 1.3 cm stretch mesh cod end liner. Although catches of pelagic fishes by bottom trawls seldom provide accurate estimates of absolute abundance of these species, they probably do reflect relative

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TABLE 1.—Catch statistics for *Decapterus punctatus* in the South Atlantic Bight. n = number of trawls; $\bar{x}_{st}$ = stratified mean catch tow^{-1}; $\bar{x}_{ln}$ = stratified mean catch tow^{-1} for ln(x + 1) transformed data; $\bar{x}_{Bliss}$ = Bliss (1967) estimate of the stratified mean catch tow^{-1}; CV = coefficient of variation for untransformed data; CV_{ln} = coefficient of variation for ln(x + 1) transformed data.

Cruise	n	$\bar{x}_{st}$	$\bar{x}_{ln}$	$\bar{x}_{Bliss}$	CV	CV_{ln}
Fall 1973 (23 Oct.-16 Nov.)	67	2.83	0.59	1.86	31.6	1.68
Spring 1974 (1 Apr.-9 May)	89	1.21	0.25	0.58	35.8	1.70
Summer 1974 (13 Aug.-19 Sept.)	69	3.13	0.59	1.97	25.5	1.69
Winter 1975 (16 Jan.-2 Feb.)	52	0.24	0.11	0.79	0.8	2.02
Spring 1975 (31 Mar.-10 Apr.)	40	0.08	0.06	0.07	0.4	1.31
Summer 1975 (30 Aug.-19 Sept.)	68	1.17	0.37	0.89	7.9	1.47
Winter 1976 (12 Jan.-7 Feb.)	69	1.73	0.17	0.52	62.4	2.81
Summer 1976 (28 Aug.-21 Sept.)	69	1.51	0.34	0.87	25.7	1.70
Winter 1977 (17 Jan.-9 Mar.)	72	3.30	0.14	1.18	197.0	9.01

abundance and distribution (Wenner et al. 1979a). All trawling was conducted from the RV *Dolphin*, a 32.6 m converted tug, for approximately 30 minutes at 6.5 km/hour. Weight and fork length (FL) were measured for each individual, except for large catches which were subsampled. Surface and bottom temperatures were taken after each tow.

Length-frequency distributions were compared by season and by depth zone. An index of relative abundance (IRA = $1/n \sum \ln(x + 1)$; n = # trawls in each depth zone, x = weight of fish for each tow) was calculated from the catches for each depth zone (Musick and McEachran 1972). The stratified mean catch per tow and the estimated variance of the stratified mean catch per tow (Cochran 1977) were calculated from untransformed and ln (x + 1) transformed data to reduce the effects of contagion (Elliott 1971). The coefficient of variation was used to compare variation in catches (Clark and Brown 1977). The Bliss (1967) approximation retransformed the data from logarithmic to arithmetic units. The Wilcoxon rank sum statistic (Hollander and Wolfe 1973) was used to compare catches, depths, and temperatures of sponge-coral (Wenner 1983) and sandy open-shelf (Struhsaker 1969) habitats. Habitat designations of Wenner et al. (1979a) were used. Catches collected north and south of lat. 31°30′N were compared for winter and summer cruises to determine if seasonal migration occurred.

Reproductive Biology

Specimens used for reproductive analyses were collected in 1980 by several research and commercial vessels, frozen, and examined in the laboratory. Specimens were measured (nearest mm) and weighed (nearest 0.1 g). Ripe ovaries were fixed in Gilson's solution (Bagenal and Braum 1978) for fecundity determination. All other gonads were fixed in formol-alcohol, stained with a modified Harris hematoxylin and counterstained with eosin (Humason 1972). Maturity stages for testes follow Hyder (1969); maturity stages for ovaries were based on Wallace and Selman (1981) and the frequency distributions of oocyte diameters. Frequency distributions of oocyte sizes were determined from randomly selected ovaries in each maturity stage. Analysis of variance revealed no differences in means and variances of oocyte diameters taken from different regions of ovaries in any stage. Therefore, oocyte distributions for each ovary were determined from two or three randomly selected sections.

Proportions of fish in each maturity stage were determined bimonthly, and gonadosomatic indices [GSI = gonad wt/(body wt – gonad wt)] were determined for each maturity stage (except stage 1 when gonadal tissues weighed <0.1 g).

Ova numbers were estimated by modifying the methods of Macer (1974). Both ripe ova and developing oocytes with diameters >0.115 mm were counted. Developing oocytes were included in fecundity estimation because they exhibited characteristics of secondary growth phase (Wallace and Selman 1981) and were atretic in spent ovaries.

Feeding Habits

Stomach contents of 457 fish collected in 1980 were fixed in 20% formalin, and stored in 50% isopropyl alcohol. Frequency of occurrence (%FO) and percentage composition by number (%N) were computed for major prey categories. Volumetric displacement (%VOL) of prey categories from a representative subsample of 30 stomachs were determined by using a 0.1 cm^2 grid (Windell 1971). Seasonal and ontogenetic change in diets were compared with an index of relative importance [IRI = (%N + %VOL)(%FO)], computed from the sums of each prey category (Pinkas et al. 1971).

Feeding periodicity was determined by plotting the percentage of empty stomachs collected per time period, using 377 stomachs with known collection times. Distributions of fish lengths collected in dif-

ferent time intervals were compared to evaluate size bias that may occur with this method (Jenkins and Green 1977).

Age and Growth

Utricular otoliths (lapilli) of specimens collected in 1980 were used for age determination. Otoliths were stored in 95% ethyl alcohol and prepared for viewing using a modification of the methods of Haake et al. (1981), which resulted in a thin sagittal section containing the core of the otolith embedded in "Spurr" (Spurr 1969). Otolith length was measured to the nearest 0.1 mm at 100× with an ocular micrometer. Otolith images were projected on a high resolution television screen with a high resolution camera, which produced a total viewing magnification of 1088× or 2176×. Otoliths examined by scanning electron microscopy were prepared by the methods of Haake et al. (1981). Two counts of growth increments were made by the author, and an additional count was made by other experienced readers. Mean counts were used in all analyses, and specimens were discarded if individual counts for a specimen differed by more than 10%. Different readers usually showed agreement between counts: percentage difference between readers averaged 8%.

Counts of otolith increments were obtained from 71 juvenile and adult round scad, 13-143 mm FL. Sixty specimens (121-180 mm FL) could not be assigned ages because of the numerous growth interruptions in outer regions of the otolith. Increment formation was validated by examination of the margins of otoliths of juveniles (13-55 mm FL) collected at different times of day. Consistent measurements of the marginal increment could not be made because of the irregular shape of the lapilli; thus, only the occurrence of an incremental or discontinuous zone (terminology of Mugiya et al. 1981) could be noted.

The SAS NLIN regression procedure with DUD and Marquardt options (Helwig and Council 1979) was used to determine parameters for the von Bertalanffy (1957) and Gompertz (Zweifel and Lasker 1976) growth equations. Because similar patterns of variation were observed in plots of the residuals of both models, r^2 values were used to evaluate model performance (Grossman et al. 1985). Instantaneous growth rates (%FL d^{-1} and %WT d^{-1}) were calculated according to Ricker (1979). Weights were converted from lengths by using the least squares regression (Sokal and Rohlf 1981), ln wt (in g) = 2.96 ln FL (in mm) − 11.2 (r^2 = 0.99), determined from 156 individuals (13-185 mm FL) randomly selected within 10 mm size classes from all specimens (total = 1047) collected in 1980.

RESULTS

Seasonal Distribution and Relative Abundance

A total of 57,460 round scad were captured at 230 of the 739 stations in depths from 11 to 267 m; over 99% of the catch came from <92 m. Fish ranged from 2 to 26 cm FL ($\bar{x}$ = 11.4), with 99% of the fish 6-17 cm FL.

Round scad were more widely distributed and abundant in summer and fall than in winter and spring. Indices of relative abundance (Fig. 1) were consistently high in summer and fall at shallow depths (<55 m) where *D. punctatus* were captured at 121 of 220 trawl stations. Indices of relative abundance during summer and fall in 56-110 m depths were quite variable, and catches in waters >110 m were rare (3 of 78 trawls), small (52 individuals captured), and occurred only in summer. The highest indices in winter and spring occurred in 19-110 m depths (usually 19-27 m), but were lower than values in summer and fall. Round scad were rarely collected in 9-18 m depths and never collected in waters >110 m in winter.

Differences among untransformed ($\bar{x}_{st}$), transformed ($\bar{x}_{\ln}$), and Bliss ($\bar{x}_{\text{Bliss}}$) estimates of the stratified mean catch per tow (Table 1) revealed additional seasonal changes in the distribution of round scad. Transformed and Bliss estimates of the stratified mean catch per tow were higher in summer and fall than in winter and spring. However, untransformed values ($\bar{x}_{st}$) indicated that total catches in winter often exceeded total catches in summer. Such differences in catch statistics resulted from the relatively high frequency and low variability of catches in summer and fall, and the relatively low frequency and high variability of catches in winter and spring. This result was generally consistent with the coefficients of variation (CV and $CV_{\ln}$), which indicated increased clumping in the winter catches.

The seasonal distribution of round scad appeared affected by temperature (Table 2). Over 97% of winter catches occurred in waters warmer than 15°C, over 99% of spring catches were made in waters warmer than 17°C, and over 99% of summer and fall catches occurred in waters warmer than 20°C.

Habitat affected the distribution of round scad in

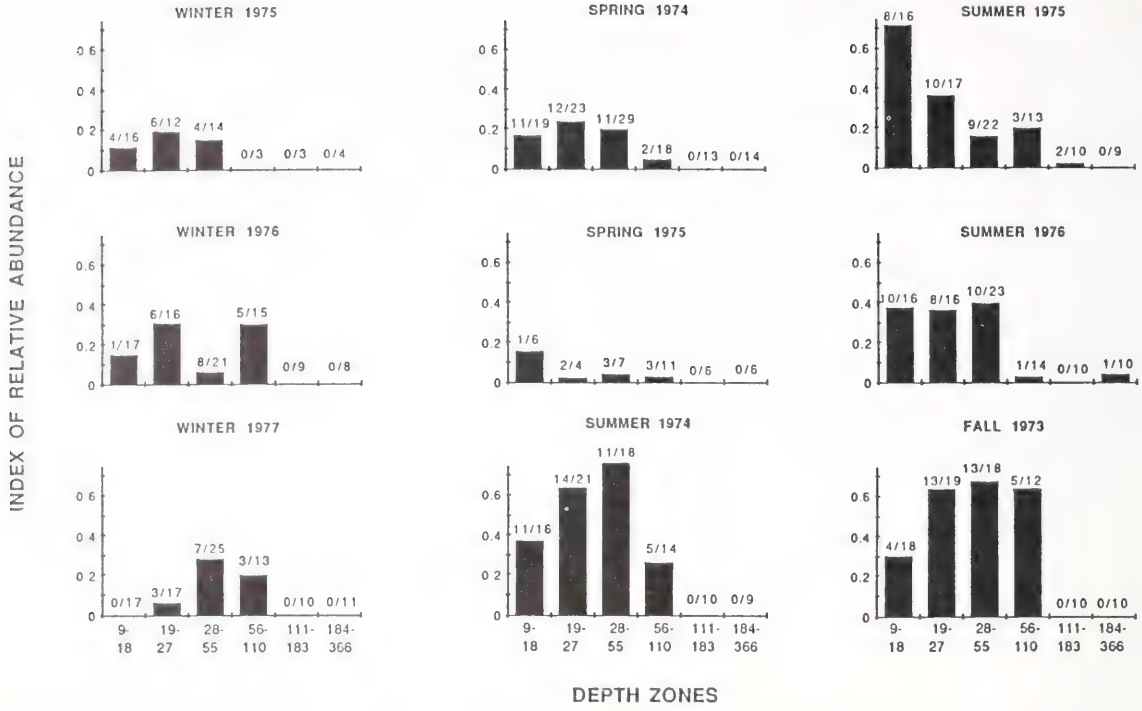

FIGURE 1.—Indices of relative abundance (Musick and McEachran 1972) of *Decapterus punctatus* by depth zone from MARMAP trawl survey for all cruises. Fractions are the number of trawls with round scad/total number of trawls.

TABLE 2.—Surface and bottom temperatures where *Decapterus punctatus* was collected in the South Atlantic Bight. Upper figure of each pair is surface value, lower figure is bottom value; $\bar{x}$ = mean, s = variance.

	Winter			Spring		Summer			Fall
	1975	1976	1977	1974	1975	1974	1975	1976	1973
$\bar{x}$	17.4	19.1	17.9	19.6	18.7	27.9	28.1	26.0	23.8
	17.2	17.0	16.4	19.1	17.4	25.5	25.4	25.4	23.7
s	2.5	3.5	2.5	1.5	2.7	0.5	0.6	0.6	1.9
	2.0	2.8	2.1	1.3	1.3	1.9	4.9	3.5	1.9
mini-	13.3	12.1	11.5	17.4	14.9	26.9	26.9	26.0	17.2
mum	13.3	12.3	11.6	17.0	14.9	19.3	9.8	8.5	17.2
maxi-	21.7	23.3	18.9	23.2	23.8	29.1	29.3	28.7	26.5
mum	19.9	22.8	18.9	22.0	19.2	28.2	29.2	27.4	26.3

winter. Catches over sponge-coral habitat were significantly larger than catches over sandy habitat in winter during 1976-77, whereas catches over the two bottom types were similar in other seasons (Table 3). Habitat types did not differ in temperature during either winter (Wilcoxon rank sum tests, P = 0.25 and 0.20, df = 19 and 12, respectively). Thus, temperature alone did not appear to account for the observed difference in winter catches over the two bottom types.

TABLE 3.—Comparison of catches of *Decapterus punctatus* over sponge-coral and sand habitats by cruise. If the Wilcoxon rank sum (Z) is significant (*), the direction of the difference is indicated. ΣC_l = sum of catches over sponge-coral habitats (n_l = # trawls), ΣC_s = sum of catches over sand habitats (n_s = trawls).

Cruise	ΣC_l	n_l	ΣC_S	n_s	Z	
Winter						
1975	3	(3)	672	(49)	0.23	
1976	7,201	(11)	597	(75)	3.57*	(L>S)
1977	10,936	(11)	39	(82)	5.40*	(L>S)
Spring						
1974	239	(11)	4,717	(91)	0.05	
1975	2	(6)	46	(34)	0.36	
Summer						
1974	445	(14)	8,023	(74)	0.61	
1975	614	(18)	4,805	(69)	0.92	
1976	663	(8)	5,094	(81)	0.86	
Fall						
1973	215	(10)	13,139	(77)	0.74	

Round scad did not appear to undertake seasonal longshore migrations in the South Atlantic Bight. Catches north and south of lat. 31°30′N (which roughly bisects the South Atlantic Bight) showed occasional differences (Table 4), but no consistent

seasonal pattern. Catch differences indicative of a southward migration in winter and northward in summer (either N < S in winter and spring or N > S in summer and fall) occurred only in winter 1975 and summer 1976. Distributions opposite to the above patterns occurred in summer 1975. Similarity in the numbers (Chi-square test, $P = 0.50$, 1 df) of gill rakers, a variable character (Berry 1969), from specimens collected off South Carolina in winter ($\bar{x} = 37.2$, $s^2 = 1.2$, $n = 33$) and summer ($\bar{x} = 36.9$, $s^2 = 1.4$, $n = 38$) also suggested that discrete stocks were not migrating through the South Atlantic Bight.

Although adults and juveniles were caught at all depths throughout the year, length-frequency distributions by depth (Fig. 2) showed a similar pattern for nearly every cruise: fish size decreased from 9-18 m to 19-27 m depths, then increased with increasing depth to 110 m. Catches in 9-18 m consisted primarily of adults in fall and winter, whereas both juveniles and adults were captured in spring and summer. Juveniles predominated in 19-27 m, whereas adults composed most of the catch in deeper waters.

TABLE 4.—Comparison of catches of *Decapterus punctatus* north and south of lat. 31°30′N by cruise. If the Wilcoxon rank sum (Z) is significantly different (*), the direction of the difference is indicated. ΣC_n = sum of the catches north (n_n = # trawls north), ΣC_s = sum of the catches south (n_s = # trawls south).

Cruise	ΣC_n	n_n	ΣC_s	n_s	Z	
Winter						
1975	8	(17)	667	(35)	561.80*	(S>N)
1976	6,149	(42)	1,649	(44)	0.07	
1977	10,728	(48)	247	(45)	0.31	
Spring						
1974	993	(62)	3,963	(40)	0.33	
1975	44	(36)	4	(4)	0.25	
Summer						
1974	1,892	(47)	6,576	(41)	0.15	
1975	1,915	(49)	3,504	(38)	1.35*	(S>N)
1976	4,395	(46)	1,362	(43)	2.52*	(N>S)
Fall						
1973	6,184	(47)	7,170	(40)	0.85	

Reproductive Biology

All stages of ovarian maturity had different frequency distributions of oocyte diameters (Fig. 3). Resting ovaries contained primary or first growth phase oocytes approximately 25-115 μm in diameter. Few larger (>115 μm) developing or atretic oocytes occurred. Oocytes in developing ovaries ranged from 30 to 375 μm in diameter, and exhibited characteristics of first or second growth phase. Either one or two modes were present in the frequency distributions of the sizes of second growth phase oocytes, 100-375 μm in diameter. Germ cells in ripe ovaries ranged from 30 to 495 μm in diameter. Ripe ovaries contained oocytes in both growth phases and maturing ova. Two or three modes were present in the frequency distibution of germ cells of ripe ovaries. Spent ovaries contained small oocytes in primary growth phase and occasionally larger oocytes undergoing atresia. Germ cells in these flaccid ovaries were usually 30-255 μm in diameter, although larger cells were observed. Gonadosomatic indices (Table 5) changed as expected: indices increased from resting through ripe stages, then decreased for spent fish.

Maturity stages of testes were more difficult to distinguish because testes often contained all stages of spermatogenesis; therefore, stage determination was based upon subjective interpretation of the relative quantities of spermatocytes, spermatids, and sperm. Although more variable, gonadosomatic indices of males (Table 5) were similar to those of females.

TABLE 5.—Gonadosomatic indices (gonad wt/(total body wt − gonad wt)) of *Decapterus punctatus* by stage maturity. $\bar{x}$ = mean, s = variance, n = sample size.

	Testes			Ovaries		
	$\bar{x}$	s	n	$\bar{x}$	s	n
Resting	0.008	0.004	64	0.007	0.003	60
Developing	0.018	0.012	103	0.027	0.011	49
Ripe	0.028	0.014	74	0.045	0.019	64
Spent	0.015	0.009	18	0.016	0.008	13

Seasonal occurrence of maturity stages showed good agreement between males and females (Fig. 4), and indicated a protracted spawning period. Developing gonads were found from February through August, and ripe individuals of both sexes were collected from March through August.

Examination of gonads indicated that both species mature at approximately 110 mm FL. Frequency distributions of length by sex (Fig. 5) indicate that both sexes mature over a narrow size range. Specimens <100 mm FL were immature, whereas more than 90% of fish 110-119 mm FL were mature. Both ripe males and females were collected in the size range at which gonadal development begins (100-109 mm FL).

Fecundity estimates (# ova female^{-1} yr^{-1}) for 32 ripe females (119-174 mm FL) ranged from 6,200 to 51,000 per female and were highly variable for specimens of similar sizes. The distribution of the sizes of the oocytes in these ovaries was not deter-

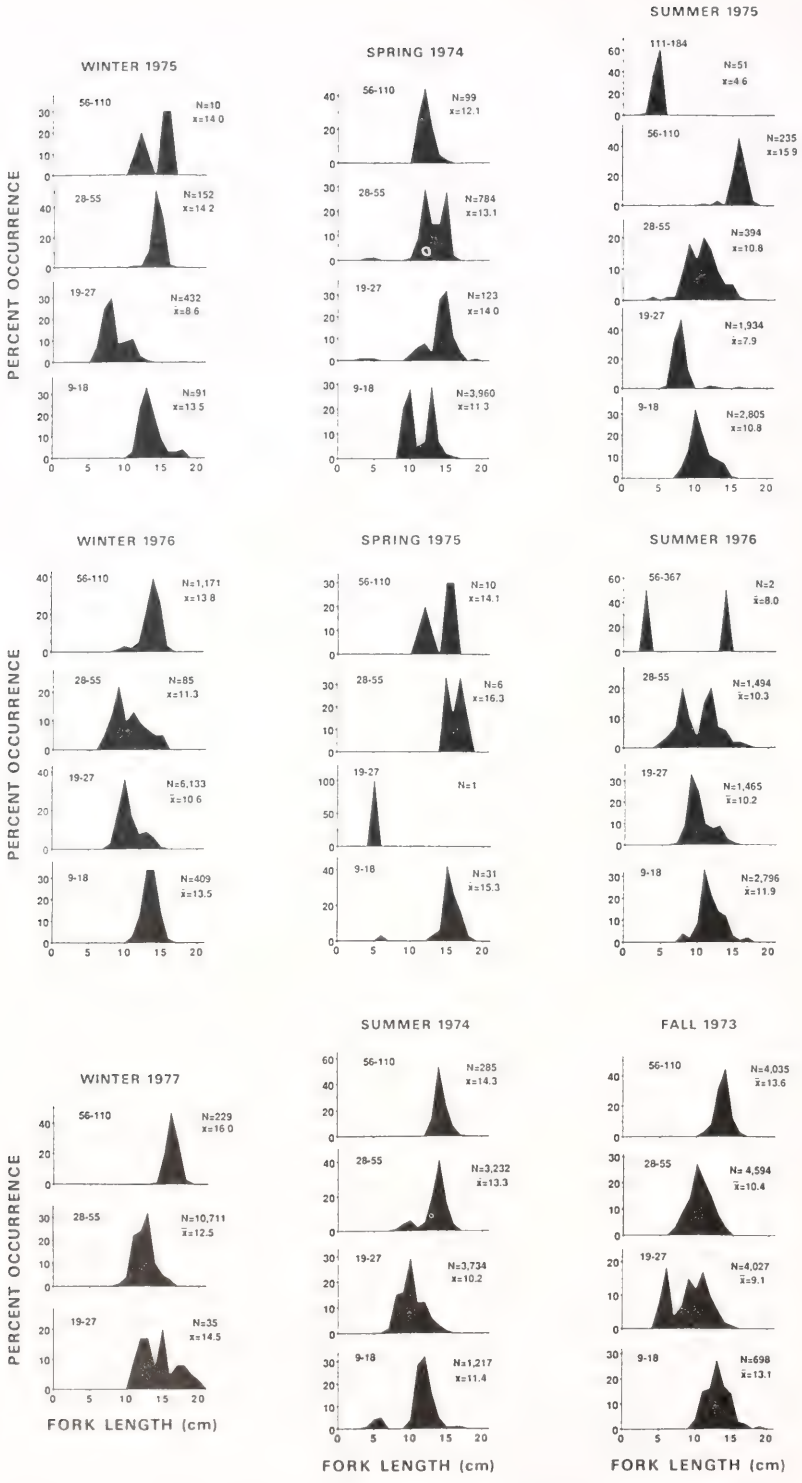

FIGURE 2.—Frequency distributions of fork lengths of *Decapterus punctatus* by depth zone, for all cruises. Numbers above each distribution indicate range of the depth zone in m; N is sample size; $\bar{x}$ is mean length of individuals.

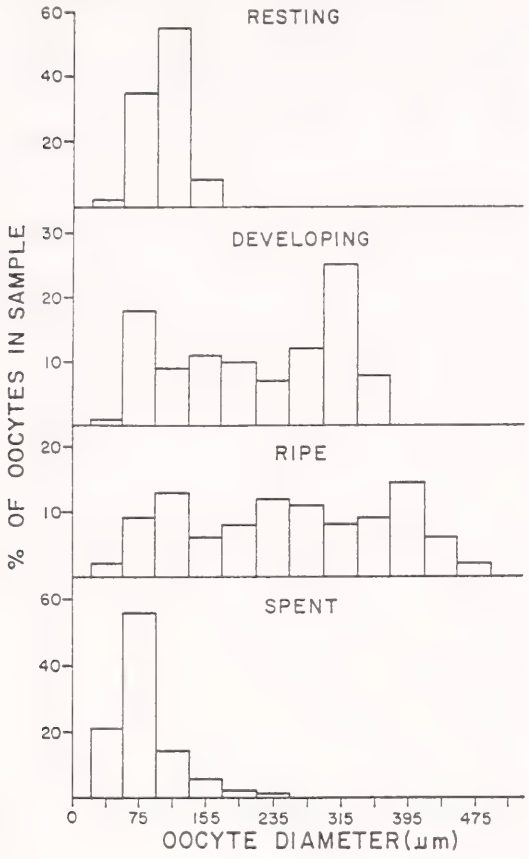

FIGURE 3.—Frequency distributions of oocyte diameters from four randomly selected ovaries of *Decapterus punctatus* in each maturity stage. The total number of oocytes measured in each ovary was 306 (oocytes from 3 sections within the anterior, central, and posterior regions of each ovary).

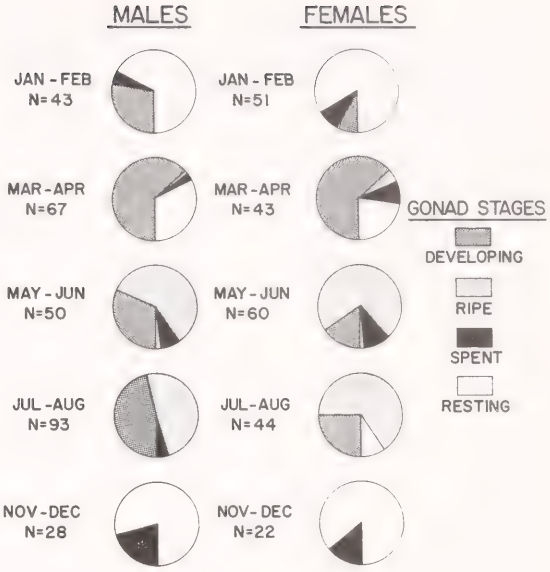

FIGURE 4.—Seasonal occurrence of maturity stages of gonads of *Decapterus punctatus*. N is sample size for each bimonthly period. No gonads were examined from specimens collected in September and October 1980-81.

mined, and it was unknown if these individuals had spawned. The regression equations of fecundity on length and weight for 33 specimens were as follows: $\log_{10}$ fec = $-10.9 + 5.63 \log_{10}$ FL ($r^2 = 0.46$); and $\log_{10}$ fec = $-1.14 + 1.56 \log_{10}$ wt ($r^2 = 0.55$).

Feeding Habits

Approximately 91% of round scad (39-189 mm FL) contained identifiable prey. The highest indices of relative importance for all specimens were for copepods (0.37), mollusk larvae (0.19), amphipods (0.06), and ostracods (0.04). The most numerous prey groups were mollusk larvae (29%, predominantly gastropod and pelecypod veligers), copepods (25%), barnacle cyprids (14%), and ostracods (10%). Chaetognaths (35%), copepods (28%), mollusk larvae

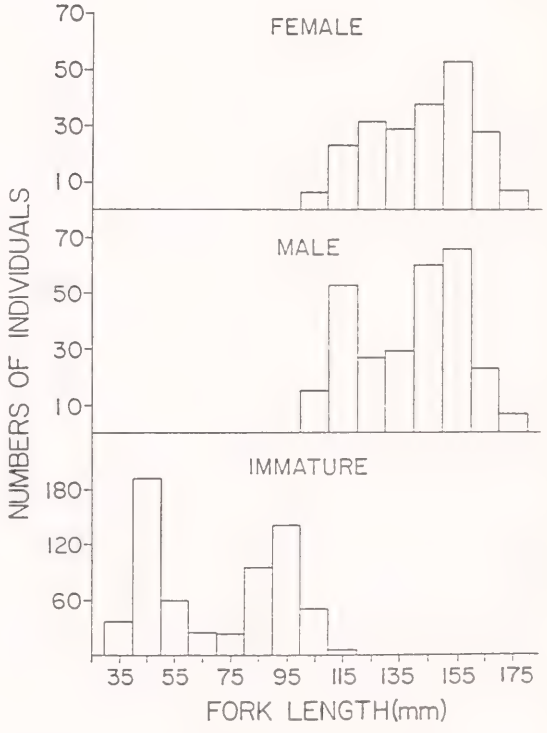

FIGURE 5.—Frequency distributions of fork length of *Decapterus punctatus* by sex. Both sexes mature at approximately 110 mm FL.

(12%), and amphipods (10%, predominantly hyperiids and caprellids) contributed the greatest volumes of prey. Copepods (70%), mollusk larvae (47%), amphipods (30%), and decapod larvae (25%) occurred most frequently.

Some differences were found in stomach contents of fishes of different size (Table 6). Small fish preyed almost exclusively on copepods. Medium-sized fish preyed predominantly on copepods, but less frequently and to a lesser extent than small fishes. Large fish fed on a variety of prey and consumed large prey items (such as chaetognaths).

Mollusk larvae and copepods dominated the diets in all seasons except spring (Table 7). In spring, round scad fed on copepods, ostracods, chaetognaths, and barnacle cyprids. The preponderance of copepods in diets of round scad in summer is due in part to the large number of juveniles included in the analysis. The mean size of fish in the summer sample was smaller than the mean size of fish in all other seasons (Student-Newman-Keuls tests; $q_{453.4}$ = 14.1 for winter vs. summer, $q_{453.3}$ = 13.2 for summer vs. spring, and $q_{453.2}$ = 11.1 for summer vs. fall). In all other seasons, dietary analyses (Table 5) were based on fish samples with similar size distributions (Student-Newman-Keuls tests; $q_{453.3}$ = 0.7 for winter vs. fall, $q_{453.2}$ = 0.7 for winter vs. spring, and $q_{453.2}$ = 0.1 for fall vs. spring). The mean number of prey items showed considerable seasonal variation from 4.6 in fall to 104 in spring.

The percentage of empty stomachs varied as a function of time of day (Fig. 6). Few empty stomachs (2-7%) were collected from midmorning to early evening, whereas 13-29% of stomachs were empty from early evening to midmorning. Size effects are unlikely to have caused the observed differences in the percentages of empty stomachs: samples with lower (2, 5, and 7) and higher (13, 20, and 29) percentages were comprised of fish of similar size (ANOVA, $F_{(1,4)} \doteq 0.01$, $P > 0.75$).

Age and Growth

Validation of the daily growth marks on otoliths of round scad was provided in two ways. Examination of marginal increments of lapilli from small specimens (13-55 mm FL) collected at different times of day suggested daily periodicity of increment formation. The margin consisted of the transparent incremental zone from midafternoon until early morning and the dark discontinuous zone in midmorning (Table 8). The allometric relationship between otolith and fish length also validates the use of otoliths for age determination. Otolith length (OL)

TABLE 6.—Index of relative importance (IRI), frequency of occurrence (%FO), volumetric displacement (%VOL), and relative abundance of prey (%*N*) by sizes. *N* = sample size (# empty stomachs), $\bar{x}$ = mean fork length in mm, *s* = variance of fork lengths, and *n* = total number of prey.

Length/prey	*N* %	VOL %	FO %	IRI
40-89 mm FL: *N* = 82(12), $\bar{x}$ = 50 mm, *s* = 13 mm, *n* = 1,272				
Copepoda	74	80	75	1.15
Mollusca	13	5	24	0.04
Decapoda	3	7	27	0.03
Amphipoda	2	2	15	0.01
Eggs	3	2	24	0.01
Ostracoda	1	1	10	<0.01
Other	4	3	32	0.02
90-139 mm FL: *N* = 192(15), $\bar{x}$ = 114 mm, *s* = 13 mm, *n* = 8,003				
Copepoda	34	57	74	0.67
Mollusca	20	13	47	0.16
Cirripedia	31	13	20	0.09
Ostracoda	9	8	22	0.04
Amphipoda	2	3	28	0.01
Decapoda	1	3	25	0.01
Other	3	3	32	0.02
140-189 mm FL: *N* = 183(14), $\bar{x}$ = 156 mm, *s* = 10 mm, *n* = 12,850				
Mollusca	36	12	59	0.28
Copepoda	14	12	64	0.17
Amphipoda	14	12	31	0.08
Chaetognatha	15	53	10	0.07
Ostracoda	11	5	30	0.05
Cirripedia	4	2	25	0.02
Decapoda	1	1	32	0.01
Other	5	4	48	0.04

TABLE 7.—Frequency of occurrence, volumetric displacement, and relative abundance of prey of *Decapterus punctatus* by season. Abbreviations as in Table 6; r = range of fork lengths.

Season/prey	N %	VOL %	FO %	IRI
Winter: N = 116(10), $\bar{x}$ = 140 mm, s = 25 mm, r = 85-185 mm, n = 4,357				
Mollusca	47	32	48	0.38
Copepoda	17	31	52	0.25
Ostracoda	15	14	31	0.09
Cirripedia	12	5	33	0.06
Decapoda	2	7	35	0.03
Amphipoda	1	2	17	0.01
Other	6	9	47	0.07
Spring: N = 112(5), $\bar{x}$ = 135 mm, s = 18 mm, r = 97-175 mm, n = 10,999				
Copepoda	21	18	92	0.36
Amphipoda	17	15	52	0.16
Ostracoda	13	6	45	0.09
Chaetognatha	17	51	13	0.09
Cirripedia	22	5	25	0.07
Mollusca	6	2	67	0.05
Decapoda	1	2	26	0.01
Other	3	2	45	0.02
Summer: N = 161(16), $\bar{x}$ = 87 mm, s = 40 mm, r = 35-163 mm, n = 6,505				
Copepoda	55	73	79	1.01
Mollusca	37	18	43	0.24
Decapoda	1	3	22	0.01
Amphipoda	1	1	21	<0.01
Ostracoda	1	1	10	<0.01
Cirripedia	1	1	9	<0.01
Other	2	2	28	0.01
Fall: N = 68(10), $\bar{x}$ = 138 mm, s = 33 mm, r = 48-180 mm, n = 264				
Mollusca	65	44	21	0.23
Copepoda	19	34	42	0.22
Other	16	22	36	0.14

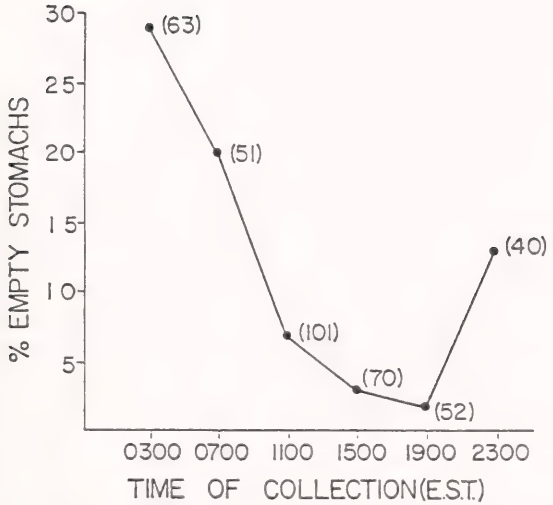

FIGURE 6.—Percent of empty stomachs of *Decapterus punctatus* collected at different times of day. Samples were pooled over 4-h intervals, of which midpoints are given. (n) is sample size.

TABLE 8.—Appearance of marginal increments of otoliths of *Decapterus punctatus* collected at different times of day. Data indicate increments are formed daily. N = number of specimens, times are Eastern Standard Time.

FL of specimens (N)	Time of capture	Marginal increment
42-55 mm (4)	0239-0257	wide, transparent
17-22 mm (11)	0812-0817	thin, dark
13-24 mm (4)	1506-1516	wide, transparent
35-53 mm (8)	2045-2053	wide, transparent

was proportional to fork length throughout the size range (14-143 mm FL) for which age determination was possible ($\log_{10}$ OL (in mm) = 0.82 $\log_{10}$ FL (in mm) − 1.61; r^2 = 0.99, n = 71).

The thickness and structure of growth increments changed in consistent ways in lapilli (Fig. 7). Ten to twelve faint daily increments surrounded a central core, which contained the primordium (Fig. 8). The next 10-15 increments increased in thickness, and the following 20-25 increments gradually decreased in thickness. A distinct change occurred at this point, and increments became thinner and more regular. Increments appeared uniform in thickness

FIGURE 7.—Sagittal section through a lapillus of *Decapterus punctatus*. The pattern of fine, regular growth increments is interspersed increasingly with heavy, irregular growth interruptions (crosshatches) in outer regions of the otolith. Bar indicates 0.10 mm, P is the primordium.

FIGURE 8.—Scanning electron micrograph of a sagittal section through the primordium of a lapillus of *Decapterus punctatus*. P is the primordium and crosshatches denote daily increments. The pattern of otolith growth of juveniles was consistent in most otoliths.

to approximately increment 100, then gradually became thinner and more difficult to count. Growth interruptions appeared in outer portions of otoliths of large fish, and growth records were more irregular.

Round scad grew rapidly for 120-150 days until reaching sexual maturity at approximately 110 mm FL (Fig. 9). The von Bertalanffy [FL = 161 (1 – exp (–0.012 (age – 29.5)))] and Gompertz [FL = 1.17 exp [4.76 (1 – $e^{-0.026\,(age)}$)]] growth equations provided good and nearly identical fits (r^2 = 0.96 and 0.97, respectively) to the observed data. Specific growth rates (Table 9) for juveniles were initially high, decreased sharply until sexual maturity, then decreased more gradually throughout the time period for which age determination was possible. The largest specimen for which reliable counts could be determined was 143 mm FL, although most specimens at that size could not be assigned an age.

The age of round scad for the entire size range (FL up to 21 cm) that was collected in the South

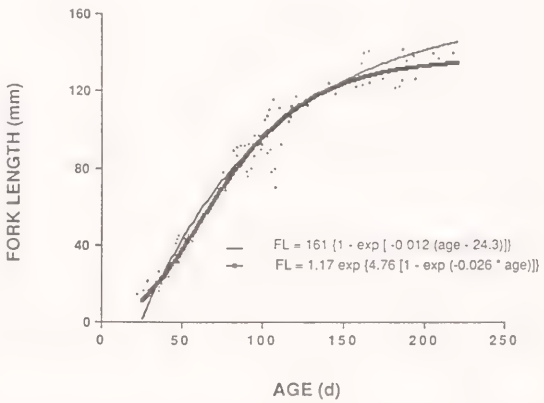

FIGURE 9.—Von Bertalanffy (thin line) and Gompertz (heavy line) growth equations. Sexual maturity of *Decapterus punctatus* is reached at approximately 110 mm FL in 120-150 days.

Atlantic Bight could not be determined from daily increments on the lapillus. The age of all specimens <120 mm FL could be determined, but only half of

TABLE 9.—Instantaneous growth rates (Ricker 1979) of *Decapterus punctatus* predicted from the von Bertalanffy equation (fig. 11). Weights were converted from lengths by using the regression: ln Wt (g) = 2.96 ln FL (mm) – 11.2.

Age (d)	FL d^{-1} (%)	Wt d^{-1} (%)
35-60	6.3	13.2
61-85	1.9	5.6
86-105	0.8	2.6
106-130	0.7	2.2
131-155	0.4	1.6
156-180	0.3	1.2

the specimens 121-143 mm FL and no individuals >143 mm FL could be assigned an age. Replicate counts of otolith increments from adults often differed by >10%, and were considered unreliable. In addition, frequent growth interruptions occurred in the outer portions of the otoliths of large specimens, and the timing of formation of such marks was not known.

DISCUSSION

Seasonal Distribution and Relative Abundance

Round scad apparently migrate shoreward across the continental shelf as sea temperatures increase in spring, then migrate into warm (>15°C) midshelf (28-110 m) depths as inshore temperatures decline in winter. Intermediate shelf depths in the South Atlantic Bight are fairly warm year round, unlike inshore waters which are seasonally cooled by cold fronts (Atkinson et al. 1983) and outer shelf waters which are intruded upon by cold-water upwellings (Blanton et al. 1981). Magnuson et al. (1981) reported that catches of round scad were proportional to temperature, and laboratory studies (Wyllie et al. 1976) have suggested a preferred temperature of 27°C. Seasonal onshore and offshore movements are made by round scad in the Gulf of Mexico (Klima 1971) and by other pelagic fishes in the South Atlantic Bight (Wenner et al. 1979a, b, c, d, 1980) and elsewhere (Allen and DeMartini 1983).

Longshore migration does not appear to be a consistent feature of the movements of round scad along the southeastern Atlantic states. Differences of catches (Table 4) made north and south of lat. 31°30′N are inconsistent, and limited meristic data (see Results) provides no evidence of movements by discrete stocks through the South Atlantic Bight. Although fish communities of live bottom habitats may change (Chester et al. 1984), latitudinal differences in the distribution of demersal fishes in sandy, open shelf habitats of the South Atlantic Bight are not apparent (Wenner et al. 1979a). More substantive information (tag-recapture studies, etc.) than the limited data given above is needed to determine accurately the movement patterns of round scad. At the present time, available information suggests that seasonal migration in round scad involves mainly onshore or offshore movement.

The abundance of round scad in the South Atlantic Bight is undoubtedly underestimated by catch statistics (Table 2). First, benthic otter trawling is generally inadequate for determining the abundance of small, mobile pelagic species (Wenner et al. 1979a). Second, the attraction of round scad to sponge-coral habitats in winter may have exaggerated the apparently large fluctuations in the seasonal abundance of round scad in the South Atlantic Bight. The sampling protocol assumes equal probability of capture over the different habitat types, but the probability of capturing round scad over live-bottom habitats varies seasonally. An increased proportion of live-bottom areas should be sampled in winter to obtain more reliable estimates of the abundance of round scad. The distribution, extent, and adequacy of sampling of live-bottom habitats are not well known (Wenner 1983). Thus, sampling inadequacies and the seasonal attraction of round scad to live-bottom habitat result in underestimation of abundance.

Several factors may influence the attraction of round scad to live-bottom habitat in winter. First, round scad utilize live-bottom habitat in winter, when invertebrate biomass has peaked and potential competitors and predators have decreased (George and Staiger 1978[3]; Wenner et al. 1980, 1983, 1984; Sedberry and Van Dolah 1984). Second, winter temperatures at live-bottom stations, though not significantly different from temperatures at sand-bottom stations, tend to be warmer, and scad prefer warm waters. The greatest densities of round scad occur in the midshelf where seasonal temperatures are generally warmest and the most highly productive live-bottom areas are located (Miller and Richards 1980; Sedberry and Van Dolah 1984). Finally, the relief of live-bottom habitats (albeit low) may serve to attract round scad; many coastal pelagic fishes, including round scad, have an affin-

[3]George, R. V., and J. C. Staiger. 1978. Epifaunal benthic invertebrate and demersal fish populations in the Georgia Bight continental shelf environment. South Atlantic Benchmark program, Volume 3, Texas Instruments Inc. Draft Report, p. 211-254.

ity for structure (Klima and Wickham 1971; Feder et al. 1974; Hastings et al. 1976).

Although fish sizes within each depth zone overlapped, the observed pattern was fairly consistent and distinct for all cruises; adults composed the catch in 9-18 m depths, and fish in deeper waters (mostly juveniles) showed a positive size-depth correlation. Adults migrate inshore in spring to feed and spawn, and offshore in winter to avoid cold waters. However, the apparent movement of juveniles to deeper waters is not understood. Correlations between fish size and depth are numerous in aquatic habitats (Helfman 1978), but explanations based on changing physiological tolerances (Bullis and Struhsaker 1970), foraging strategies (Polloni et al. 1979), and predation responses (Hobson 1972) have been difficult to demonstrate in most fishes.

Reproductive Biology

Although results (Fig. 3) indicate that *D. punctatus* spawn primarily from March through August, spawning probably occurs through September and to a lesser extent throughout the year. Collections were not made during September and October of 1980, but water temperatures in August and September in the South Atlantic Bight are generally similar (Atkinson et al. 1983). Round scad larvae have been collected in winter in the South Atlantic Bight (Fahay 1975; Powles and Stender 1976) and the eastern Gulf of Mexico (Leak 1981). Larval occurrence has been correlated with water temperature in the eastern Gulf of Mexico (Leak 1981), and sufficient water temperatures (>20°C) occur throughout the year in parts of the South Atlantic Bight.

The pattern of oocyte development is generally quite variable and complex in serial spawners: oocytes develop asynchronously or synchronously in groups, and ova are released in batches. Three observations suggested that round scad are serial spawners: 1) the occurrence of three distinct modes in the frequency distributions of oocyte diameters from ripe ovaries collected in spring; 2) two modes in those distributions from ripe fish collected in late summer; and 3) evidence of spawning in ovaries having a frequency distribution of oocyte diameters similar to developing ovaries. Spawning was indicated by disorganized ovarian septa with conspicuous spaces, debris in the ovarian lumen, residual atretic oocytes, and brown bodies.

Although estimates of fecundity in round scad are comparable to those of *D. pinnulatus* (Yamaguchi 1953), *D. macrosoma*, and *D. russelli* of similar size (Tiews et al. 1970), the conventional method applied here probably underestimated fecundity. Because gonads used in fecundity estimation were not examined histologically, it was not possible to determine if spawning had occurred recently in specimens used for fecundity measures. In addition, sufficient numbers of specimens were not examined to determine spawning frequency from running-ripe (DeMartini and Fountain 1981) or postovulatory (Hunter and Goldberg 1979) females. Previous studies on other serial spawning fishes (Hunter and Goldberg 1979; Hunter and Leong 1981; DeMartini and Fountain 1981; Conover 1985) have shown that estimates of annual fecundity (total number of ova spawned in 1 year) can differ from conventional fecundity estimates (which ignore multiple spawning) by an order of magnitude. Serial spawning fishes generally have low relative ovary weights (Martinez and Houde 1975; Smith and Lasker 1978; DeMartini and Fountain 1981), but can expend over 100% of their body weight per year in eggs (Hubbs 1976; DeMartini and Fountain 1981). If observed fecundity in round scad (6,200-51,000) is extrapolated from the 4.3% relative ovary weight (Table 7) to total body weight, then fecundity estimates of 142,000-1,173,000 would result. If observed fecundity is divided by the proportion of oocytes in the most advanced developmental mode (32%, from Figure 3), then batch fecundities of approximately 2,000-16,000 per female (130-230 eggs/g body weight) and annual fecundity estimates (based on 10 d spawning cycle for 6 months) of 36,000-288,000 would result. Both estimates are entirely speculative, but support the contention that the conventional method underestimated fecundity, and emphasize the need for additional studies on the fecundity of round scad.

Round scad mature at a smaller size than reported for other species of *Decapterus*, which reach maturity at 18-20 cm (Yamaguchi 1953; Tiews et al. 1970). The small size at which round scad become sexually mature suggests that they are under strong selection pressure to mature rapidly. The natural mortality of round scad in the eastern Gulf of Mexico is high (Houde et al. 1983). Compared with temperate and boreal species, many tropical clupeoids also mature at small sizes, seldom attain large size and have high adult mortality rates (Blaxter and Hunter 1982; Houde et al. 1983).

Feeding Habits

Zooplanktivores feed during the day or at night, but seldom during both periods (de Silva 1973; Hob-

son and Chess 1976; Helfman 1986), probably due to visual limitations (Durbin 1979). The absence of nocturnal prey and the strongly diurnal periodicity of stomach fullness (Fig. 6) indicate that *D. punctatus* feeds during the day. Round scad rarely consumed mysids, tanaids, and cumaceans, which are abundant in the water column at night but dwell in the benthos during the day (Kaestner 1970; Hobson and Chess 1976). The diel periodicity in empty stomachs (Fig. 6) is not biased by sizes of fish differing among collection times (see Results). Individuals of different sizes have similar gut evacuation rates (Perrson 1981) but different gut capacities; therefore, small individuals empty their guts more quickly than large individuals. The lack of a size difference in this analysis substantiates the daily feeding period by round scad.

Scales were a common item in round scad stomachs, but were deleted from analyses because several observations indicated that round scad were feeding on debris (including scales) generated by trawling: 1) oral chambers of specimens often contained scales; 2) scale size and type varied; and 3) the extent of presumed lepidophagy was not correlated with fish size. In addition, scales were seldom found in latter portions of the gut. Most other lepidophages generally prey on a small number of species (Sazima 1983), or for only a portion of their life history (Carr and Adams 1972). Thus, round scad probably consume scales on occasion, but not to the extent that the data would indicate. It seems likely that round scad were feeding on scales abraded from fishes during their avoidance of or capture by the trawl. Yamaguchi (1953) also attributed the occurrence of scales in the stomachs of *D. pinnulatus* to gear bias.

Ontogenetic changes in the diet occurred with growth. Larger individuals had more diverse diets which included larger prey. Small fish fed primarily on small, abundant copepods and copepodites. Stomach contents of several (10) small juveniles (13-26 mm FL) collected during an ichthyoplankton survey in 1973 also contained mostly copepods (S. Hales pers. obs.). Data from these specimens were not included in previous analyses due to the possibility of differential prey digestion.

Seasonal changes in the diets of round scad probably reflect fish size and the relative abundance of zooplankton components. Copepods and mollusks were the most important prey in all seasons except during spring when barnacle cyprids were the most numerous and chaetognaths contributed the greatest volume of prey. Zooplankton volumes and diversity reach their peak in the spring (Deevey 1960; Reeve 1964), and cyprids are more abundant in the spring than in any other season (Lang and Ackenhausen-Johns 1981). The preponderance of copepods in the diet of round scad in summer partially reflects the abundance of juvenile round scad, which appear to feed primarily on small abundant copepods.

Molluscan veligers may be an exception to the general pattern of prey selection. They have not been reported to be abundant in the zooplankton of the South Atlantic Bight (Paffenhöfer 1980, 1981) or elsewhere (Deevey 1960; Reeve 1964), yet occurred frequently in the diets of round scad. Shells of both gastropods and bivalves and the opercula of gastropods were all that remained in the stomachs of round scad on occasion; such parts are apparently digested slowly and retained in the stomach. However, such an explanation alone does not account for the frequency and abundance of mollusk veligers. Brewer and Kleppel (1986) have reported the paradox of low bivalve density yet frequent occurrence in the guts of some larval fishes, and suggested that bivalve veligers may occur in microscale patches just above the bottom. Planktonic stages of gastropods are important prey for horse mackerel (*Trachurus trachurus*), which school near the bottom (Macer 1977). Thus, the frequency and abundance of mollusk veligers in the stomachs of round scad may be attributed to both the abundance of mollusk veligers being greater than generally recognized and their low digestibility and long retention in stomachs.

Age and Growth

Round scad grow rapidly to sexual maturity at 11 cm FL in 4-5 months, and apparently achieve a major proportion of their total size in their first year. Because of the problems encountered in age determination in this study, little can be said about the age of most adults. The asymptote predicted by the von Bertalanffy model (161 mm FL) is much shorter than the maximum size observed in the South Atlantic Bight. Thus, the growth rates observed in this study should not be extrapolated to older and larger fish. Houde et al. (1983) reported the mean size of round scad in the eastern Gulf of Mexico to be 136 mm FL at age 1, 160 mm FL at age 2, and 177 mm FL at age 3. In addition, they reported considerable variation (10-20 mm) in the mean lengths at age. Differences in the growth rates observed in the two studies are believed to be due mainly to methodology, but may also be due to slight differences in the growth of round scad between the two areas.

Growth rates reported in this study for juvenile round scad are similar to those of juvenile *Selar crumenopthalmus* (Kawamoto 1973) and *Trachurus trachurus* (Macer 1977), and would enable spring-spawned round scad encountering favorable conditions to spawn in the fall (Leak 1981). Other species of *Decapterus* are reported to grow more slowly (Yamaguchi 1953; Tiews et al. 1970; Ingles and Pauly 1984), but such studies used length-frequency information only and may have underestimated growth. These species (*D. pinnulatus*, *D. russelli*, *D. macrosoma*) reach sexual maturity at 17-20 cm FL in their first or second year, and attain 25-35 cm FL in 3-5 years (Yamaguchi 1953, Tiews et al. 1970). The rapid growth of round scad to sexual maturity suggests that this species is under strong selection to mature early. Mortality estimates for round scad (Leak 1981; Houde et al. 1983) are high even in comparison with other coastal pelagic fishes, which do not achieve as large a size as round scad during their first year.

Daily growth increments were easily distinguished in juveniles and small adults, but could not be used to determine ages of most adults. Frequent spawning involving the high energetic expenditures reported for other pelagic fishes (Hubbs 1976; DeMartini and Fountain 1981) would result in slow growth of adults. Specific growth rates based on Houde et al. (1983) (0.04% FL d^{-1} for 1-2 yr olds, and 0.03% FL d^{-1} for 2-3 yr olds) are much slower than the rate of young adults (0.28% FL d^{-1}) observed in this study. A reduction in increment thickness with growth (Brothers 1979; Campana 1985) might result in the exceedingly fine increments observed in the outer portions of the otoliths of adults. Another possibility is that growth of adults is insufficient to maintain the pattern of daily increment formation. McGurk (1984) has reported that daily increment formation in larval *Clupea harengus* may be altered when absolute growth rates are <0.36 mm d^{-1}.

Occurrence of growth interruptions in the outer portions of otoliths of most adults also hindered age determination. The period of formation of such marks was not known. If such marks are not formed in 1 day, then inclusion of such marks as daily increments would result in underestimation of the ages of adults. Growth interruptions may result from spawning (Panella 1974), lunar or tidal rhythms (Rosenberg 1982), or stress (Ralston and Miyamato 1983); however, correlations between such events and the growth record of round scad could not be determined.

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A COMPARISON OF THE AGE AND GROWTH OF THE TIGER SHARK, *GALEOCERDO CUVIERI*, FROM OFF VIRGINIA AND FROM THE NORTHWESTERN GULF OF MEXICO[1]

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ABSTRACT

Lengths at age and growth rates for the tiger shark, *Galeocerdo cuvieri*, in the northwestern Alantic and Gulf of Mexico were estimated from bands formed seasonally in the vertebral centra. The tiger shark grows rapidly compared with many other shark species. Growth rates for Gulf of Mexico juveniles were faster than for Atlantic juveniles. This produced significantly different ($P < 0.01$) estimates of the parameters of von Bertalanffy curves for the two regional samples. With sexes combined, parameter estimates for the Gulf of Mexico sample were $L_\infty = 388$ cm TL, $K = 0.184$, $t_0 = -1.13$ years; for the Atlantic sample they were $L_\infty = 440$ cm TL, $K = 0.107$, $t_0 = -2.35$ years. Males mature at approximately 310 cm TL, females at 315-320 cm TL, but the regional differences in juvenile growth rates result in different ages at maturity. In the Gulf of Mexico, males mature in 7 years, females in 8 years; in the Atlantic, males and females both mature in approximately 10 years. The largest male and female examined (381 cm TL) were 15 and 16 years of age.

The tiger shark, *Galeocerdo cuvieri*, is cosmopolitan in warm-temperate and tropical coastal and oceanic waters of the western North Atlantic (Castro 1983). It is usually found alone or in small groups of three to six individuals distributed rather homogeneously over most bottom types (Springer 1963). Because of its large size, it is one of the most frequent entries in recreational fishing tournaments, and it occurs regularly, but in low numbers, in longline catches (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981, 1986). Along the U.S. Atlantic coast, the tiger shark occurs year-round off Florida, migrates as far north as Cape Cod in summer (Casey 1964), and returns to more southerly latitudes in fall (Musick et al. 1985). In the Gulf of Mexico, the species occurs in coastal waters from spring through fall, and in deeper continental shelf and offshore regions year-round (Branstetter 1981, 1986).

The low catch rates and semisolitary nature of the tiger shark have hindered a comprehensive study of its biology. The tiger shark is both a scavenger (Gudger 1949; Clark and von Schmidt 1965) and euryphagous predator (Bass et al. 1975; Dodrill and Gilmore 1978). Information on the reproductive biology of the tiger shark must be gleaned from scattered observations on pregnant females taken in the Indo-West Pacific and Indian Ocean (Kauffman 1950; Bass et al. 1975) and in the northwestern Atlantic (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Age and growth rates for the tiger shark have not been reported.

Alternating opaque (calcified) and translucent (less calcified) bands form in the vertebral centra of many elasmobranchs during growth (Radtke and Cailliet 1984), and if a regular periodicity can be demonstrated for the formation of these bands throughout the life of the animal (Beamish and McFarlane 1983), they can be used to assess ages for individuals in the sample and to estimate growth rates for the population. Using these bands, age and growth data for collections of tiger sharks from Virginia and the northwestern Gulf of Mexico were developed, compared, and integrated with known life history characteristics.

METHODS AND MATERIALS

Tiger sharks were examined from research and commercial longline catches and from recreational fishing tournaments. The Atlantic sample consisted of 27 specimens taken during 1983 and 1984 summer tournaments, and 42 specimens collected in May through October on longlines fished in continental shelf waters (primarily <40 m) within a 50 km radius of the mouth of Chesapeake Bay from 1977 to 1983. The Gulf of Mexico sample consisted

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of 21 specimens taken on longlines fished in continental shelf waters of the northwestern Gulf in summer and along the shelf edge in winter from 1981 to 1985. Nine more tiger sharks were examined during a summer tournament in Texas. Between 1978 and 1985, an additional 41 specimens were tagged and released between Panama City, FL and Brownsville, TX. Data on morphometrics, lengths at maturity, and weight/length relationships were supplemented by specimens collected in the north central Gulf of Mexico (Branstetter 1981) and by 23 weight/length records from specimens taken from 1976-81 Galveston, TX shark tournaments.

Measurements were taken as the straight line distance between perpendiculars with caudal fins placed in a natural position (Dodrill 1977; Branstetter 1981, 1986). The upper caudal lobe angle was calculated to be approximately 21-22°, based on a formula by Dodrill (1977) which places the vertex of the angle at the upper caudal notch. This is slightly less than the values calculated by Thompson and Simanek (1977), who measured the angle through the center of the caudal peduncle, not the upper caudal notch. Total lengths (TL) are used throughout this report, but because measurements were taken by different people, there could have been variation in placement of the long flexible upper caudal lobe into a natural angle. Therefore, for each regional sample, regressions were calculated to compare total length to the more precisely measureable fork length (FL) or precaudal length (PCL).

Weights of tiger sharks from tournaments and Virginia specimens were made with balance beam scales, and Gulf of Mexico specimens taken on longlines were weighed with spring scales. Scales were tested for accuracy between sampling periods.

Reproductive development and maturity determinations follow Springer (1960), Clark and von Schmidt (1965), and Branstetter (1981). Males were considered mature only if the claspers were fully calcified and siphon sacs were fully developed. Sperm is produced before the claspers calcify and cannot be used as a criterion of maturity. Virginity in females, indicated by the presence or absence of a hymen covering the distal end of the oviducts, is not a criterion for maturity. Females were considered mature when developing or ripe eggs were in the ovary, eggs or embryos were present in the uteri, or by uterine expansion of nongravid females.

For age and growth analysis vertebrae were removed from 25 females (125-381 cm) and 19 males (156-381 cm) from off Virginia, and from 10 females (91-355 cm) and 7 males (140-340 cm) from the Gulf of Mexico. An additional eight Gulf of Mexico specimens (100-285 cm) had been processed for sale, and sex could not be determined. A section of the vertebral column was removed from under the origin of the first dorsal fin or, when sampling commercial operations, from the cervical region dorsal to the branchial chamber. Samples were frozen or preserved in 10% formalin and stored in ethyl or isopropal alcohol. Following methods detailed in Branstetter and McEachran (1986), individual centra were cleaned and a sagittal section cut from the center. Sections were polished on wet 400 grit sandpaper and observed with a binocular dissecting microscope using transmitted light. To block incidental light, an opaque tube was placed over the section between the microscope stage and objective.

Distinct marks (annuli), as illustrated in Casey et al. (1985: fig. 1) and Branstetter and Stiles (in press: fig. 1), were visible in the intermedialia of centrum sections. These annuli corresponded to translucent areas in the corpus calcareum and to the outer edge of translucent bands on the centrum face. The annuli formed distinct borders for the growth bands. Bands were counted without knowledge of the length of the specimen. All band counts were made by the senior author. Counts for each specimen were performed twice, and if agreement was not reached, a third count was made for comparative purposes. The distance from the section focus to each annulus, centrum dorsal radius, and marginal increment was measured on a line from the focus through the center of the intermedialia.

The periodicity of annulus formation was verified through marginal increment analysis and corroborated with comparisons to back-calculated lengths at each mark. Relative marginal increments were calculated by dividing absolute marginal increment widths by the width of the last fully formed band, and relative marginal increments were compared by month of capture. Back calculations were performed using the Dahl-Lea method (Carlander 1969) where

$$TL_i = M_i(TL)CR$$

and TL_i = total length at mark i (M_i), TL = observed length at capture, and CR = centrum radius. Back calculations were analyzed for each sample as a whole and by age class.

Tiger sharks are born in the Gulf of Mexico and along the southeastern U.S. Atlantic coast in early

summer (Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981). Therefore, for simplicity, a 1 June birthday was used to estimate actual ages. For back calculations, ages were based on the age at the formation of winter annuli; therefore, for summer caught tiger sharks, there is a difference between the actual age and the age at annulus formation (i.e., a tiger shark taken in June that was aged at 6.0 years would be 5+ years of age in back calculations). To estimate growth rates, observed age/length data were applied to a computerized von Bertalanffy growth model (Fabens 1965). Males and females were taken in similar numbers, and both sexes for both samples are represented graphically; however, because of the small data base, sexes were combined for all mathematical analyses.

Apparent differences in mean lengths at age between the two samples were tested for significance using t-tests (Snedacor and Cochran 1980), and independent von Bertalanffy curves for the two regional samples were tested for differences following methods of Bernard (1981) using computer analysis (SAS Institute 1985).

RESULTS

A FL/TL plot of data from both samples (Fig. 1) can be used for general conversions of lengths reported in this paper. However, analyzed separately, the two regional samples had nonsignificantly different regression formulas for the relationships of FL or PCL to TL:

Gulf

FL = 0.871(TL) − 13.5 (n = 33, r = 0.998)
PCL = 0.788(TL) − 12.1 (n = 34, r = 0.977)

Atlantic

FL = 0.853(TL) − 10.1 (n = 66, r = 0.994)
PCL = 0.797(TL) − 14.2 (n = 68, r = 0.992)

Combining data for both samples, the relationship of centrum radii (CR) to length (TL) (Fig. 2) could be described by linear regression:

$$TL = 14.72\ CR + 51.15 \quad (n = 64,\ r = 0.972)$$

Although the regression did not pass through the origin, no correction factor, such as the Fraser-Lee method (Carlander 1969), was applied because this factor did not adequately describe the rapid embryonic growth (Casey et al. 1985; Branstetter 1986). For simplicity, this isometric relationship was used for back-calculating lengths at previous ages and did not produce Lee's phenomenon (Table 1). However, the relationship was slightly curvilinear and was more accurately described by separating the data into immature vs. mature specimens (< or > 310 cm):

Immature - TL = 17.7 CR + 20.18 (n = 44, r = 0.972)
Mature - TL = 7.6 CR + 190.21 (n = 20, r = 0.796).

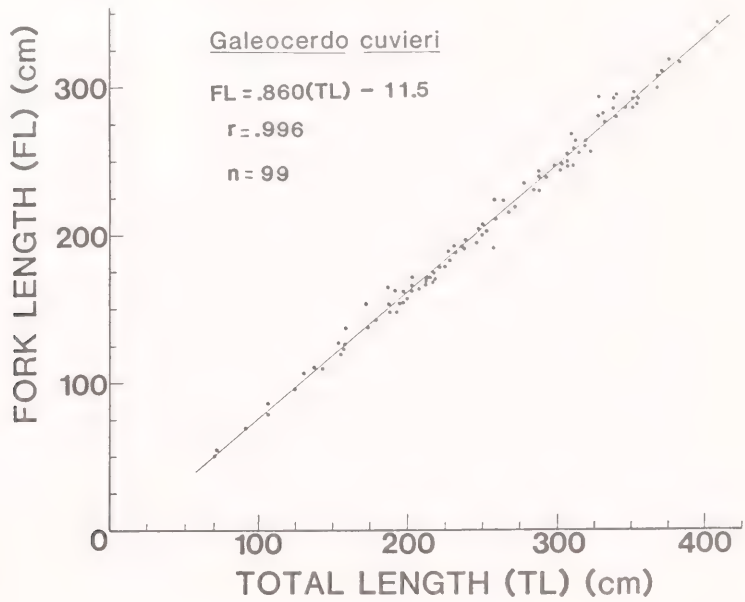

FIGURE 1.—Relationship between fork length and total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast.

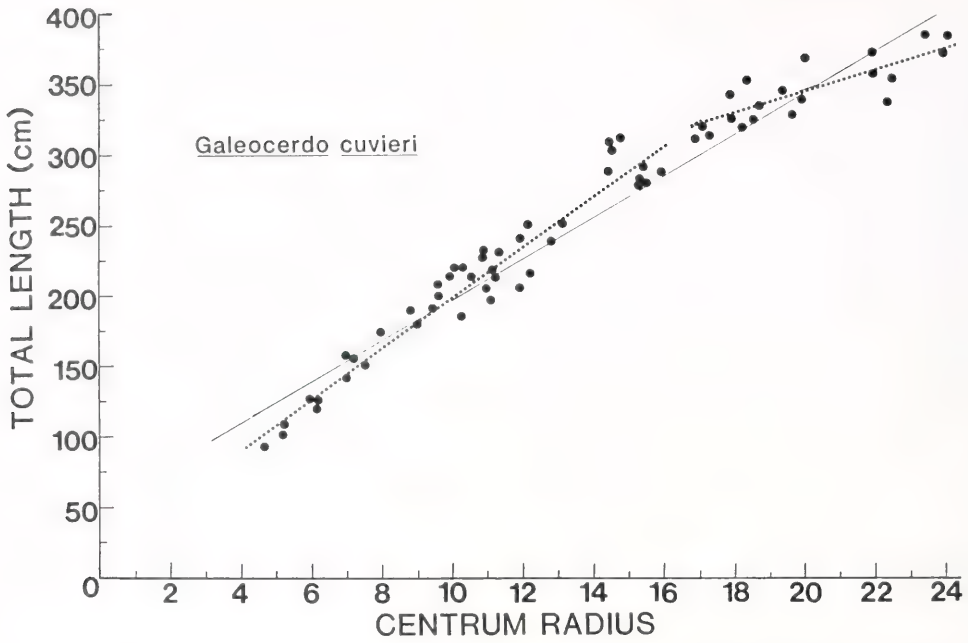

FIGURE 2.—Relationship of centrum dorsal radii to total length for *Galeocerdo cuvieri* taken in the Gulf of Mexico and off the Virginia coast. Centrum radii measurements are in ocular micrometer units (omu). 1 omu = 1.2 mm. See text for discussion of the different regressions.

Neonatal tiger sharks had only one annulus. Back calculations of length at the formation of this annulus indicated that it was formed at birth. Prebirth marks, which formed at placentation (Radtke and Cailliet 1984; Casey et al. 1985; Branstetter 1987c; Branstetter and Stiles in press), were not found in this aplacentally developing species; a condition also noted for the aplacental *Alopias vulpinus* (Cailliet et al. 1986).

Marginal increment analysis on all but neonatal tiger sharks (Fig. 3) indicated that the annuli formed in late fall or early winter (October-December) became visible off the centrum edge by January and were farthest from the centrum edge in summer. This "winter" annulus was consistent throughout the size range of the sample (Beamish and McFarlane 1983). Therefore, the first band bordered by the birth mark and the first winter annulus represented approximately 6 months growth; remaining bands formed annually.

Annuli along the periphery of centra in large (old) tiger sharks were closely spaced, making counts for these individuals more difficult. Annulus counts between the two readings were identical except for some of the larger individuals. In these cases, results of a third count matched one of the two previous counts, and this was the value accepted.

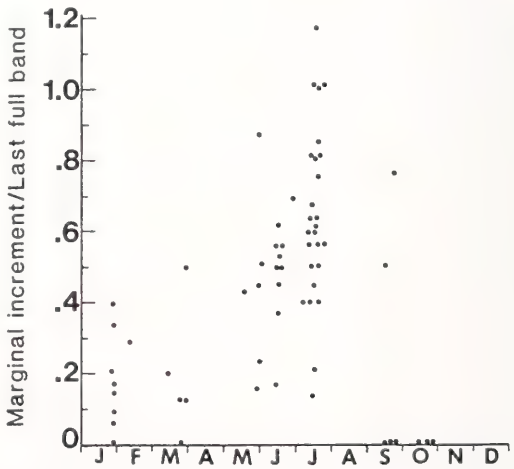

FIGURE 3.—Marginal increment widths as a ratio of the width of the last fully formed band in vertebral centra of *Galeocerdo cuvieri* compared by month. Specimens from the two regional samples are combined.

The two regional samples of tiger sharks exhibited similar growth rates. By combining observed length at age data from both samples a single von Bertalanffy curve could be fitted by using Fabens (1965)

TABLE 1.—Back calculations by age class for the Virginia and Gulf of Mexico samples of tiger sharks, *Galeocerdo cuvieri*. Ages are based on age at the formation of the winter mark. Lengths to nearest cm TL. Significantly different mean lengths at age between samples indicated by asterisks (** $P < 0.001$; * $P < 0.01$).

Winter mark	*n*	Age at the formation of the winter mark																
		B	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+
0	0	—																
1	2	76	126															
2	2	74	130	156														
3	6	73	125	159	185													
4	9	73	122	161	189	209												
5	1	84	126	160	192	219	237								ATLANTIC			
6	2	78	135	178	205	223	244	262										
7	2	75	120	151	186	218	243	259	274									
8	2	82	118	163	198	224	242	261	278	294								
9	1	73	122	148	165	196	224	249	271	290	309							
10	5	72	116	154	186	211	229	250	270	290	305	314						
11	6	72	121	159	184	211	239	262	280	300	316	326	336					
12	1	78	118	144	176	211	230	245	270	284	296	311	322	330				
13	1	73	128	183	219	238	256	284	302	317	326	335	348	356	366			
14	1	62	107	153	187	207	253	270	281	299	314	324	337	345	351	362		
15	2	77	123	158	189	214	236	261	287	301	313	325	334	346	355	364	372	
16	1	72	111	150	180	198	214	244	260	274	285	304	318	331	346	359	364	378
$\bar{X}$		74	122	159**	188**	213**	237**	258**	277**	295*	310*	321	334	342	355	362	369	378
cm/yr		[1](48)	37	29	25	24	21	19	18	15	11	13	8	13	7	7	9	
cm/yr		[1](49)	51	35	29	24	18	18	17	16	13	9						
$\bar{X}$		73	122	173**	208**	237**	261**	279**	297**	314*	330*	343	352					
0	1	77																
1	4	70	114															
2	3	74	129	169														
3	5	74	125	180	212													
4	2	80	124	170	214	241												
5	2	77	125	169	208	235	267											
6	1	68	115	166	198	227	256	281										
7	2	74	130	172	197	233	249	274	288									
8	1	61	105	179	202	229	250	275	300	307								
9	2	74	126	178	209	237	263	280	301	317	329							
10	0	—	—	—	—	—	—	—	—	—	—	—	—					
11	1	68	113	166	215	254	283	290	306	316	333	343	352					

[1]Six months growth.

procedure (Fig. 4) to adequately describe the growth rate. However, young age classes in the Gulf of Mexico (hereafter referred as Gulf) sample were slightly larger at age than their Atlantic counterpart. Independent von Bertalanffy curves for each data set had different parameter estimates. Regressions of the curves, linearized by log transformation, were analyzed for covariance (SAS Institute 1985) and were significantly different ($P < 0.0001$). Simultaneous nonlinear regression analysis of the two von Bertalanffy curves derived from back-calculated mean lengths at age produced parameter estimates with nonoverlapping simultaneous confidence intervals (Bernard 1981).

Back calculations by age class for each sample (Table 1) also showed the more rapid growth of the Gulf juveniles. Mean lengths at the formation of the winter annuli were significantly different ($P < 0.01$ or $P < 0.001$) for early age classes of the two samples. Neonates in both samples increased nearly 50 cm in length the first 6 months, and the Age I Gulf tiger sharks continued to grow at 50 cm/year, but Atlantic Age I individuals grew <40 cm/year. Gulf tiger sharks continued to grow approximately 4 cm/year faster than the Atlantic population until the fourth year. Growth rates then became similar; Gulf tiger sharks were simply larger at age.

Observed and back-calculated lengths at age (Table 2) corresponded within each sample. Comparisons of observed and back-calculated lengths did not indicate the occurrence of Lee's phenomenon. Differences in observed and back-calculated lengths at age were attributable to the fact that most specimens in both samples were taken in summer; therefore, observed lengths at age were larger than back-calculated lengths at age based on the winter formed annuli.

The growth rate estimated from centra was validated with one tag-recapture. A female, tagged 3 November 1978, was estimated to be 230 cm, and

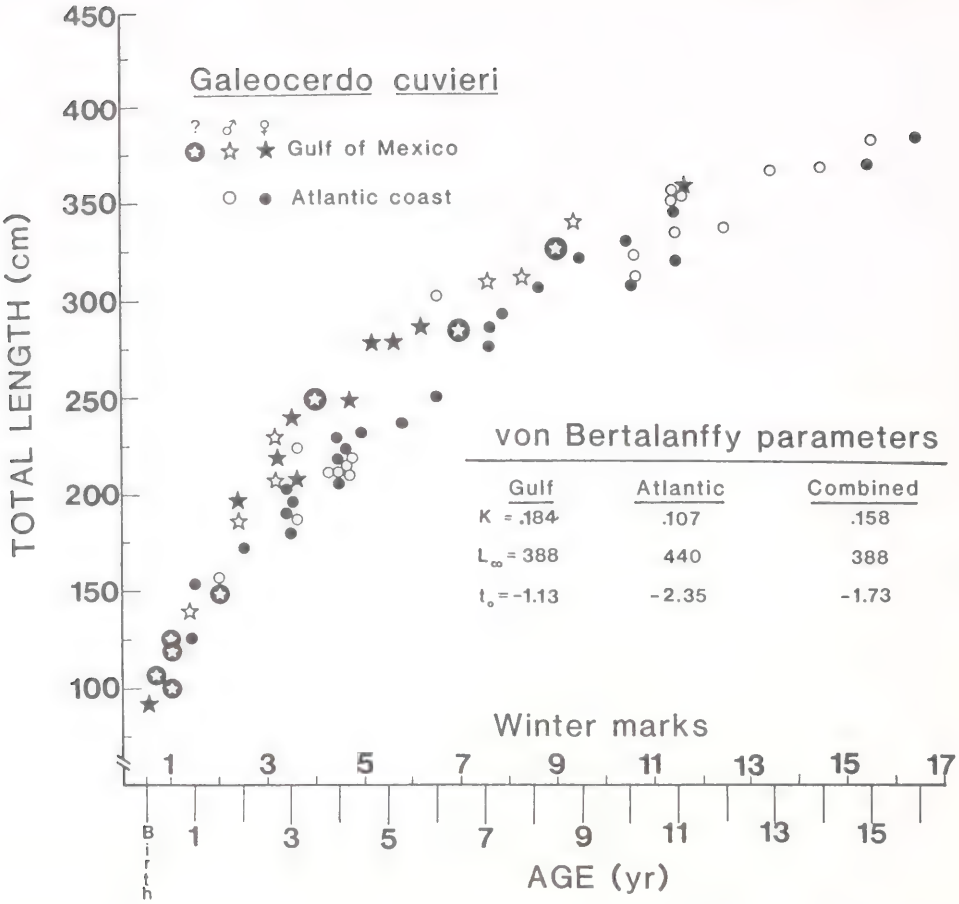

FIGURE 4.—Length at age for *Galeocerdo cuvieri* from the Gulf of Mexico and the Atlantic coast of Virginia. Individuals are plotted by their estimated actual ages (time elapsed since formation of the last winter mark). Birthdays set at 1 June.

at recapture, 7 April 1984, was estimated to be 320 cm from the weight/length relationship. The tiger shark grew 90 cm in 5.4 years. By using the age/length relationship estimated by the growth curve (Fig. 4), the shark would have been 3.4 years of age when tagged and 8.8 years of age at recapture.

Even with the relatively rapid growth rate exhibited by this species, a length-frequency analysis for both samples (Fig. 5) did not distinguish age classes. The size distribution did indicate that young juvenile tiger sharks occur only rarely in the Virginia region.

Males matured at approximately 310 cm, females at 315-320 cm, and the differences in growth rates between the two samples meant that they reached maturity at different ages. For the Gulf of Mexico, the smallest mature males (310, 311 cm) were 8.0 and 7.8 years old. The largest male aged (340 cm) was only 8.8 years old. Back calculations indicated that this individual grew relatively rapidly compared with smaller individuals in the sample, and the only larger male collected (363 cm) was not aged. The smallest mature female (325 cm) was 8.8 years old, the largest (355 cm) was 11.2 years old. For the Atlantic sample, two immature males (310, 311 cm) were not aged, but a 312 cm mature male was 10.1 years old. The largest male (381 cm) was 15.1 years old. The largest immature female (307 cm) was 8.1 years of age, the smallest mature females (318, 319 cm) were 9.0 and 11.1 years of age, and the largest female (381 cm) was 16.1 years old.

The rapid linear growth early in life did not correspond to a great increase in the weight of the individuals (Fig. 6). Growth from the third through the seventh winter decreased from 30 to 20 cm/year, and weights increased during this period. As the

TABLE 2.—Comparison of length at age for observed and back-calculated data for Atlantic and Gulf populations of the tiger shark, *Galeocerdo cuvieri*. Lengths are to the nearest cm TL. Values indicate low-mean-high (*n*) for each age class.

Winter mark:	0	I	II	III	IV	V
Age:	0	0+	1+	2+	3+	4+
Gulf						
observed	91-99-106 (2)	100-121-140 (4)	150-179-199 (3)	205-220-240 (5)	248-249-250 (2)	278-279-279 (2)
back calculation	50-73-85 (25)	96-122-137 (23)	149-173-184 (19)	192-208-228 (16)	225-237-254 (11)	239-261-283 (9)
Atlantic						
observed	NA (0)	125-140-155 (2)	156-165-173 (2)	180-192-225 (6)	205-216-229 (9)	237 (1)
back calculation	60-74-84 (44)	101-122-149 (44)	138-159-188 (42)	161-188-220 (40)	183-213-238 (34)	202-237-256 (25)

Winter mark:	VI	VII	VIII	IX	X	XI
Age:	5+	6+	7+	8+	9+	10+
Gulf						
observed	288 (1)	285-298-310 (2)	311 (1)	325-333-340 (2)	NA (0)	355 (1)
back calculation	272-279-290 (7)	283-297-306 (6)	307-314-318 (4)	325-330-333 (3)	343 (1)	352 (1)
Atlantic						
observed	250-276-302 (2)	278-282-286 (2)	292-300-307 (2)	318 (1)	307-322-335 (5)	319-341-354 (6)
back calculation	221-258-284 (24)	245-277-302 (22)	270-295-317 (20)	292-310-327 (18)	304-321-341 (17)	315-334-349 (12)

Winter mark:	XII	XIII	XIV	XV	XVI
Age:	11+	12+	13+	14+	15+
Atlantic					
observed	338 (1)	368 (1)	368 (1)	370-376-381 (2)	381 (1)
back calculation	340-343-356 (6)	346-355-366 (5)	359-362-369 (4)	364-369-378 (3)	378 (1)

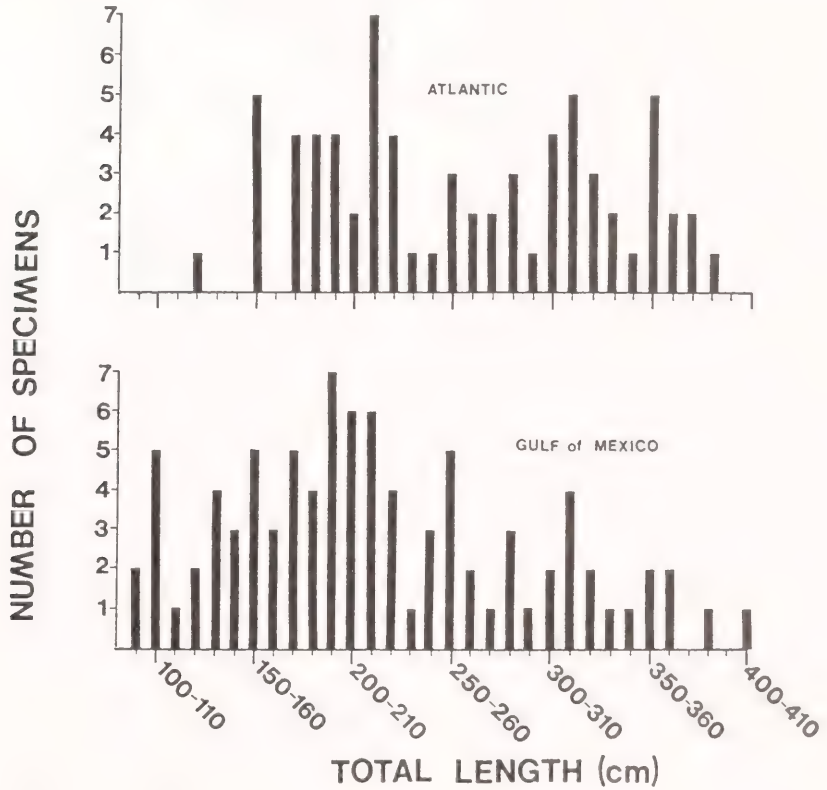

FIGURE 5.—Length frequency of *Galeocerdo cuvieri* collected off Virginia and in the Gulf of Mexico. Specimens are grouped into 10 cm size classes.

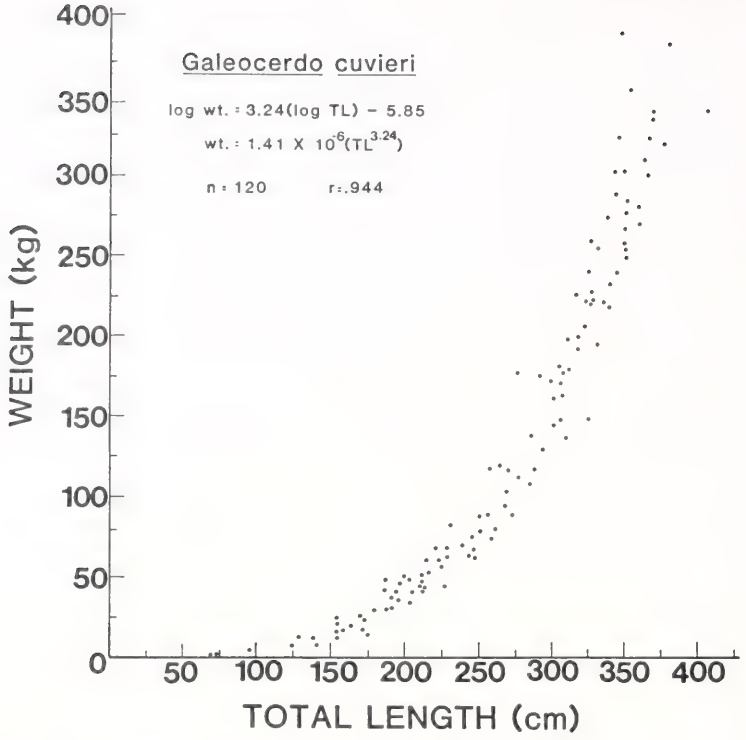

FIGURE 6.—Weight/length relationship for Atlantic and Gulf of Mexico *Galeocerdo cuvieri*, sexes combined.

animals matured at 310-320 cm, linear growth slowed from 15 cm/year to <10 cm/year, and weights increased dramatically.

DISCUSSION

An isometric relationship between centrum growth and length has been noted for many shark genera (Cailliet et al. 1983; Gruber and Stout 1983; Branstetter and McEachran 1986). The slight curvilinear relationship between centrum growth and length noted for *Galeocerdo cuvieri* suggested there were two distinct growth stanzas. A similar relationship was also noted for *Isurus oxyrinchus* (Pratt and Casey 1983). The point of inflection in the curve is generally at the length corresponding to the onset of maturity, a decreased linear growth rate and an increased weight gain rate. Apparently, centrum growth is correlated to the structural support necessary for length increases, but an increasing rate of weight gain does not require additional strengthening of the vertebral column.

Marginal increment analysis of annulus periodicity demonstrated that one growth band, consisting of one calcified opaque zone and one less calcified translucent zone, formed annually. A similar periodicity for growth bands or annuli has been verified for several shark genera (Gruber and Stout 1983; Cailliet et al. 1986; Branstetter and McEachran 1986) and validated using tetracycline injected *Negaprion brevirostris* (Gruber and Stout 1983), *Triakis semifasciatus* (Smith 1984), *Rhizoprionodon terraenovae*, and *Carcharhinus plumbeus* (Branstetter 1987a). In contrast, Parker and Stott (1965) and Pratt and Casey (1983) provided evidence that lamnoids produce two band pairs per year, and Natanson (1984) could find no regular periodicity in centrum bands of *Squatina californica*.

Our estimates indicated the tiger shark doubles in length the first year of life. This is supported by growth of a full-term embryo (69 cm) placed in an aquarium by Clark and von Schmidt (1965) on 21 May, where it survived 12 weeks growing to 89 cm.

Rapid linear growth for juvenile tiger sharks may be necessary for adequate cohort survival. With a 13-16 mo gestation period (Clark and von Schmidt 1965) and a mating season which occurs before full-term females have pupped, the female reproductive

cycle is at least 2 years. Considering the litter size (40-70 pups) (Kauffman 1950; Bass et al. 1975; Branstetter 1981), natural mortality must be high for young age classes. Pups are born in coastal waters at a relatively large size (>70 cm) which reduces some predation, but the elongate, flexible body produces an inefficient anguilliform swimming motion. Additionally, early in life, the caudal fin is extremely flexible and has a low thrust angle (Thompson and Simanek 1977). The combination of these characteristics precludes rapid swimming speeds, thus making the pups vulnerable to predation by the abundant coastal sharks including their own species. Not only does rapid linear growth make them larger than most potential predators, it may help decrease predation by increasing swimming efficiency and speed through increased body rigidity (producing a more carangiform motion) and increased caudal fin thrust angle.

Linear growth continues at >20 cm/year until the tiger sharks are near maturity. Such rapid growth is similar to that noted for several lamnoids (Parker and Stott 1965; Gruber and Compagno 1981; Pratt and Casey 1983; Cailliet et al. 1985), but contrasts sharply to the slow growth rates estimated for several carcharhinids and sphyrnids (Thorson and Lacy 1982; Gruber and Stout 1983; Schwartz 1983a). Even the more rapidly growing carcharhinids do not have such large relative increases in length (Parsons 1985; Branstetter and McEachran 1986).

The mean lengths at age between the Gulf of Mexico and Atlantic tiger sharks were significantly different, and probably represent ecophenotypic differences between the two regions. However, the two regional groups are not isolated. Our one tag-recapture was tagged off Mobile Bay, AL and recaptured in the Florida Straits off Havana, Cuba, and there are similar tag returns of tiger sharks that moved between the Gulf of Mexico and the Atlantic (J. Casey pers. commun.[4]). However, long migrations between the two regions may be restricted to larger individuals with juveniles remaining in their respective regions.

If juvenile tiger sharks do remain in their respective regions early in life, growth rate differences between the two regions may be caused by differences in early life histories. In the Gulf of Mexico, the pups apparently only migrate short distances inshore-offshore seasonally. In the Atlantic, the pups are born south of Cape Hatteras, probably in the Florida region (Dodrill 1977). These neonates may not migrate north during their first year, as small individuals, <150 cm, are rare in the Virginia region (Fig. 5). During this time, the growth rates for both groups are similar. The extensive northern migration for 1+ year old Atlantic juveniles, 150-200 cm, may be energetically costly, hindering growth. Therefore, the Gulf young that do not migrate great distances are able to attain greater lengths during this time period. The increased swimming efficiency attained with lengths >250 cm could possibly explain why growth rates become similar.

For juveniles of both regions, the energy requirements for the inefficient swimming motion and rapid linear growth apparently restrict any great increase in weight (Fig. 6). Only after the tiger sharks reach lengths >200 cm (3+ years of age) does weight increase substantially, and correspondingly linear growth begins declining. After reaching maturity (310-320 cm) linear growth is <10 cm/year while weight growth is substantial, corresponding to the change in centrum radius/length relationship (Fig. 3).

The von Bertalanffy parameter estimates for the two collections closely bracket known life history characteristics. With sexes combined, the L_∞ for the Gulf of Mexico collection and for both samples combined (388 cm) is smaller than many reported large individuals, but is a reasonable compromise between the maximum reported lengths for males and females: 419 cm individual (McCormick et al. 1964); 370 cm male, 410 cm female (Bass et al. 1975); 410 cm female (Branstetter 1981); and a 381 cm male and female from this study. However, the tiger shark is thought to attain lengths in excess of 450 cm (Bigelow and Schroeder 1948; Castro 1983), more in agreement with the L_∞ for the Atlantic sample (440 cm). The t_0 value for the Gulf sample (−1.13 years) is accurate, but the 13-16 mo gestation period is overestimated for the Atlantic sample (−2.35 years). The t_0 value for many shark species overestimates the gestation period (Casey et al. 1985; Branstetter 1986). The K values for each analysis reflect the rapid growth rate of this species and are similar to some of the more rapidly growing *Carcharhinus* species such as *C. limbatus*, *C. brevipinna* (Branstetter 1987c), *C. falciformis* (Branstetter 1987b), and *C. acronotus* (Schwartz 1983b).

At the estimated growth rate for the largest individuals (5-10 cm/year), exceptionally large specimens, 400-450 cm, would be 20-25 years of age. The

[4]J. Casey, Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882, pers. commun. June 1986.

von Bertalanffy curve using observed lengths at age produced an estimated age at L_∞ for the Gulf sample of 28 years, and 37 years for the Atlantic sample. This would mean that the species matures at 30-50% of its maximum age, and with a reproductive cycle of greater than 2 years, a female would reproduce less than 10 times. On the other hand, von Bertalanffy curves derived using back-calculated lengths at age for both samples produced estimated ages at L_∞ of 45-50 years. Exceptionally high ages at L_∞ may be due to the exponential function of the model, or it is also possible that as tiger sharks attain sizes near their maximum weight or length, centrum growth and band formation do not accurately represent age. Because no exceptionally large individuals were aged, we are unable to determine which is the case. Even so, the data indicate that the tiger shark is long-lived with a relatively low fecundity, and natural mortality for the young may be high. As with many other elasmobranchs, this combination of *K*-selected characteristics may result in an overexploitation of this species under increased recreational and commercial fishing pressure (Musick and Colvocoresses 1986).

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ECOLOGICAL CONSEQUENCES OF MECHANICAL HARVESTING OF CLAMS

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ABSTRACT

A field experiment was performed in 1,225 m^2 plots in each of two shallow estuarine habitats, a seagrass bed and a sand flat, in Back Sound, North Carolina (USA), to test the impact of clam raking and two different intensities of mechanical harvesting of clams ("clam kicking") for up to 4 years on 1) hard clam, *Mercenaria mercenaria*, recruitment, 2) seagrass biomass, 3) the density of benthic macroinvertebrates, and 4) the density of bay scallops, *Argopecten irradians*. The removal of adult hard clams with the contingent sediment disturbance had ambiguous effects on the recruitment of hard clams: in the sand flat recruitment tended to be lower (but not significantly) in intense-clam-kicking matrices than in controls, whereas in seagrass recruitment of hard clams did not not show a clear response to treatment. In the raking and light-clam-kicking matrices, seagrass biomass fell immediately by ≅25% below controls but full recovery occurred within a year. In the intense-clam-kicking matrices, seagrass biomass fell by ≅65% below levels expected from controls; recovery did not begin until more than 2 years passed, and seagrass biomass was still ≅35% lower than predicted from controls 4 years later. Clam harvest did not affect either the density or species composition of small benthic macroinvertebrates from sediment cores, probably because of their rapid capacity for recolonization and generally short life spans. In all treatments, densities of benthic macroinvertebrates (mostly polychaetes) were substantially higher in the seagrass than in the sand flat during October samplings but equal during March samplings. Bay scallop density declined with declining seagrass biomass across harvest treatments, but the intense-clam-kicking matrices contained even fewer bay scallops than their seagrass biomass would predict, perhaps because of enhanced patchiness of the remaining seagrass.

The relative inertia of the change in seagrass biomass following extensive destruction in the intensely kicked matrices suggests that seagrass replanting may be an extremely important means of returning disturbed, unvegetated areas to seagrass systems. Emergence during summer of a between-habitat gradient in infaunal densities (higher in seagrass than in sand) supports the hypothesis that seagrass provides a partial prey refuge for infaunal invertebrates. The failure of the benthic macroinvertebrate density to respond to clam harvest treatments in both sand flats and seagrass beds implies that the polychaetes which dominate recover rapidly from disturbance and are probably not adversely affected by clam harvest. The negative and long-lasting impact of intense hard clam harvest on seagrass biomass with its effects on other fisheries, including bay scallops, implies that hard clam fisheries should be managed to minimize the intensity of harvest within seagrass beds.

Technological innovation is frequently accompanied by an increased risk of harm to various aspects of the natural environment (e.g., Dickie 1974). While such innovation can be considered economically desirable and even inevitable, environmental managers still require ecological inputs to enable them to reach properly informed compromises between uncontrolled application of new technology and unnecessarily cautious protection of natural ecosystems. Because of its inherent lack of general principles and paradigms, ecology is rarely able to provide immediate answers to practical questions of the probable impact of new technology. Consequently, careful studies of the ecological impact of the application of each specific new technology are often necessary. Such studies can not only provide necessary applied information but also contribute to a better basic understanding of the specific system that is being explored.

Although fisheries biologists are renowned for managing harvests in a way that will sustain a maximum yield or maximize yield per recruit (Ricker 1975), studies are only occasionally undertaken to compare the environmental damage caused by alternative fishing gears and technologies (e.g., Caddy 1973; Peterson et al. 1983a). Such studies are most common in estuarine and other shallow-water fisheries, where high coastal productivity of diverse stocks induces intensive exploitation of a common area by multiple, potentially interfering fisheries. As technological advances in fishing gear have been made, this potential for interfishery competition has grown, as has the need for understanding the envi-

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ronmental consequences of the utilization of new, alternative technologies.

Fisheries for the hard clam, *Mercenaria mercenaria* (L.), and other sedentary benthic invertebrates require the use of either hand implements (rakes, hoes, etc.) or boat-drawn gear (dredges, trawls, etc.). Managers of benthic invertebrate fisheries may turn to the subdiscipline of benthic ecology to seek predictions of the relative environmental and ecological consequences of utilizing various alternative fishing gears or of permitting technologically new substitutions for traditional fishing methodologies. Unfortunately, benthic ecologists are frequently unable to provide confident answers to many questions, often either because the fisheries applications involve a far larger scale than can be or has been practically accommodated in basic experimental research designs or because the questions fall into an area of current debate and ongoing study in the basic science of the field.

One might take, as an example of the poor predictive capacity of benthic ecology, the question of whether widespread adoption of mechanical harvesters by commercial *M. mercenaria* fishermen will affect the future recruitment success of *M. mercenaria* in the local area of harvest. Most fisheries biologists agree that the mechanical harvesters are more efficient in gathering hard clams from a given area and cause more physical disruption of the bottom than the alternative hand methods of raking and tonging. Even given these assumed differences, benthic ecology provides mixed and conflicting predictions of the impact of switching to mechanical harvesters. Basic studies of adult-larval interactions, including some among suspension-feeding bivalves (Woodin 1976; Williams 1980; Peterson 1982b), might suggest that removal of large, adult suspension feeders would enhance the survivorship of settling larvae and thereby increase the recruitment success of *M. mercenaria* in the efficiently harvested areas. Yet, the experimental results on which such a prediction is based were achieved on a much smaller spatial scale and probably depend upon absolute density (or feeding rate) of all suspension feeders in an unspecified way. It is conceivable that the virtual removal of *M. mercenaria* over a substantial area might remove an important settlement cue (produced by adults) needed for larval habitat selection (e.g., Meadows and Campbell 1972; Gray 1974). If this were true, recruitment success of *M. mercenaria* would decline with the intensity of harvest. Similarly, benthic ecology provides conflicting predictions about the effects of the increased physical disburbance of mechanical harvesting on recruitment success of *M. mercenaria*. On the one hand, *M. mercenaria* recruits might be expected to suffer increased mortality from burial during massive sediment disturbance (Rhoads 1974; Myers 1977; Thistle 1981; Wilson 1981). Yet, larvae of many species settle more densely into disturbed bottoms (Gray 1974; McCall 1977; Hulberg and Oliver 1980). Again, these signals are conflicting but, even more importantly, experimental benthic ecology is unable to predict adequately whether the scale and intensity of disturbance during commercial clam harvesting are appropriate to invoke either of these processes.

Because of the restricted scale of past field experiments and the consequent limitations of benthic ecology in the applied arena, we designed controlled field experiments to test the impact of mechanical clam harvesting on a large scale, sufficient to provide environmental data to resource managers and to extend simultaneously the scope of basic experimental, benthic ecology. Specifically, we tested on a 1,225 m^2 scale whether the harvest of *M. mercenaria*, with its attendant physical disruption of the bottom, affected the 1) recruitment success of *M. mercenaria*, 2) biomass of seagrasses, 3) density of bay scallops, and 4) density of all other benthic macroinvertebrates. We tested these harvest effects in each of two common estuarine habitats, a sand flat and a seagrass bed, and followed not only the immediate response to harvesting but also the changes in most variables over a subsequent 3.5-yr period. Thus, the need for ecological data to use in fisheries management provided an opportunity to expand the temporal and spatial scale of experiments in marine benthic ecology and thereby evaluate our ability to extrapolate from previous theory based on smaller scales.

METHODS

To test whether the type and/or intensity of hard clam, *Mercenaria mercenaria* (L.), harvest has any detectable effect on 1) its own recruitment, 2) seagrass biomass, 3) bay scallop, *Argopecten irradians*, density, or 4) density of small benthic macroinvertebrates, we performed a large-scale field experiment at sites along the southern (barrier island) margin of Back Sound near Beaufort, NC (Fig. 1). This experiment was conducted in a seagrass meadow and in an unvegetated sand flat approximately 500 m to the west to permit a test of whether effects of harvest vary with habitat. This general area and its physical characteristics are described in several previous publications (Sutherland and Karlson 1977; Nelson 1979; Peterson et al. 1983b, 1984). Back

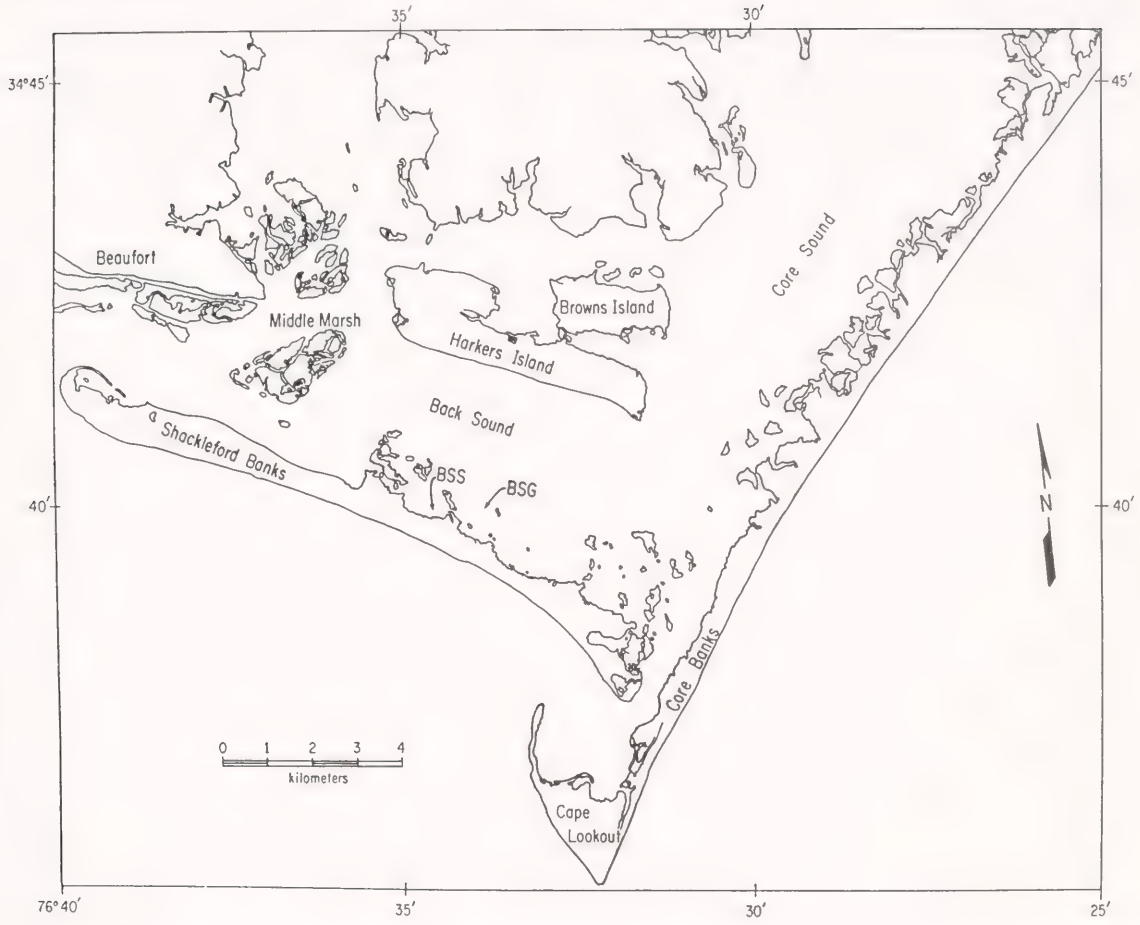

FIGURE 1.—The locations of the study sites in eastern North Carolina, near Cape Lookout. BSS indicates the sand-flat and BSG the seagrass-bed locations. Tick marks on the margins of the figure denote minutes of N. latitude and W. longitude.

Sound is a shallow marine lagoon with a lunar tide of about 0.6 m range, little salinity variation (28-34‰), and a wide seasonal temperature range from a winter monthly minimum of 2°-4°C to a summer monthly maximum of 29°-30°C. In January 1980, we selected in each habitat 6 square plots (matrices) of 1,225 m^2 area, each of which had a virtually constant water depth of about 0.1-0.3 m at low tide and homogeneous surface appearance. Specifically, all seagrass matrices held a spatially uniform cover of a seasonally varying mixture of two seagrasses, eelgrass *Zostera marina* and shoalgrass *Halodule wrightii*, whereas no sand-flat matrix contained seagrasses. These seagrass matrices had been continuously vegetated from at least 1974 until 1980 and the seagrass cover had not extended over the sand flat during that same period (Peterson et al. 1984).

Before harvest treatment, we subsampled all 6 matrices in each habitat to test whether there were any initial differences among matrices in response variables. This sampling occurred between 22 February and 31 March 1980 in the sand flat and from 1 April to 6 May 1980 in the seagrass bed. A fixed number (9 or 36) of uniformly distributed 0.25 m^2 subsamples was taken from each matrix to estimate abundance of hard clams, bay scallops, and seagrass (Table 1). A uniform sampling array was chosen to reduce the field effort and to avoid risk of sampling at or even near (<1 m) the same locations during subsequent sampling. A grid of marked ropes attached to equally spaced stakes was placed around the circumference of each matrix and moved to a new, randomly chosen set of positions for each new sampling date, thus producing a "frame shift" of the sampling template.

TABLE 1.—Temporal design of data collections and of experimental treatments for both habitats, 1980-84. Entries are numbers of samples[1] taken per matrix.

Parameter estimated	Spring 1980 22 Feb.- 6 May	Harvest treatment 12-30 May	Fall 1980 20 Oct.- 10 Nov.	Harvest treatment 19 Dec.- 22 Feb.	Spring 1981 2-13 Mar.	Fall 1981 4 Oct.- 3 Nov.	Fall 1982[2] 20-29 Oct.	Fall 1983[2] 28-31 Oct.	Fall 1984[2] 22-29 Oct.
Total hard clam density	36		36		9	36	9	9	0
Density of hard clam recruits	36		36		9	36	9	9	0
Seagrass dry mass	36		36		9	36	9	9	9
Bay scallop density	0		36		9	36	9	9	0
Density of benthic macro-invertebrates	6		6		6	6	0	0	0
Sediment size distribution parameters	3		0		0	0	0	0	0

[1]In all cases where 36 or 9 samples were taken per matrix, these were ¼ m^2 samples distributed uniformly across the matrix such that no sample fell within 1 m of any previous sample location. Where 6 or 3 samples were taken, these were chosen at random from a group of 9 uniformly distributed samples positioned in a similar way to avoid any overlaps. All sediment samples were cores of 5 cm diameter × 20 cm deep. Macroinvertebrate samples were cores of 10 cm diameter × 25 cm deep.

[2]Data taken from only the seagrass habitat on these dates.

To collect a repeatable sample, we first inserted a 0.25 m^2 circular metal sampling frame penetrating to a depth of 15 cm and used an hydraulic suction dredge to excavate the complete contents to that same depth. The material was collected in a 3 mm nylon mesh bag (for description and sampling efficiency, see Peterson et al. 1983b). All living *M. mercenaria* and *A. irradians* were removed from the mesh bag and placed in separate, labeled plastic bags for return to the laboratory. For all *M. mercenaria* we measured length in the longest anteroposterior dimension, and for all *A. irradians* we measured the distance from the flat top of the hinge to the ventral margin using vernier calipers. Seagrass material from the mesh bag was packaged in marked plastic bags in the field and returned to the laboratory, where it was gently rinsed in freshwater to remove attached salt and sediments, and dried to constant weight (2-4 days) at 105°C.

To estimate densities of small benthic macroinvertebrates, we took 9 uniformly distributed samples from each matrix in each habitat on 4 sampling dates (Table 1). We processed and analyzed a randomly chosen subset of 6 of these 9 samples for each matrix. The strategy of taking more samples than one expects to analyze is optimal when marginal costs of additional sampling are low, because extra replicates are then available for later analysis if among-sample variation proves so unexpectedly high as to reduce statistical power to an unacceptable level. Benthic invertebrates were collected using 10 cm diameter cores taken to a depth of 25 cm. Complete contents of each core were placed in separate plastic bags and gently sieved, in the laboratory, through 1 mm mesh. Sieve contents were held in bottles containing rose bengal in 10% buffered formalin until animal tissues were adequately stained and hardened. We later picked and identified to class (and to species in a subset of the samples) all animals in each sample.

In spring 1980, we also took 3 randomly located sediment cores (5 cm in diameter to a depth of 20 cm) from each matrix to characterize initial sediment conditions. Cores were transferred into individual plastic bags and frozen at −10°C until analysis of sediment size distribution by weight. We split each sample by coning and quartering (Ingram 1971) and then used standard Rotap dry sieving and pipetting procedures (Folk 1974) to estimate dry weights of sediments in each of several size classes. In addition, percent organic content was measured by weight loss on ignition at 550°C for 4 h (Gross 1981). Because our (customary) use of small-diameter cores to sample sediments failed to include large shell fragments and because such biogenic calcium carbonate appeared to be extremely common in 1 seagrass matrix, we designed a sampling procedure to estimate the relative degree of coarse shell. In October 1985, we used the suction dredge to excavate 3 haphazardly located 0.25 m^2 quadrats to a depth of 12 cm in each of the 6 matrices in each habitat. All shell fragments collected on a 3 mm

mesh were then cleaned with freshwater, dried at 60°C, and weighed to provide a quantitative indication of the relative degree of coarse shelliness in each matrix.

After our initial sampling in spring 1980, we applied harvest treatments on 2 occasions, 12-30 May 1980 and 19 December 1980-22 February 1981 with a single sampling of response variables in between (Table 1). We then sampled on 5 subsequent occasions to test for the existence and persistence of any treatment effects without applying any additional harvest treatments (Table 1). Of the 6 matrices in each habitat, 2 were left untouched as controls, 2 were given intense applications of "clam kicking", and the remaining 2 were subjected to lower but equal harvest intensities (judged by estimated percentage of spring 1980 *M. mercenaria* removed) of different types ("clam kicking" in one and hand raking in the other). Clam kicking is a mechanical form of clam harvest (described in detail in Guthrie and Lewis 1982) practiced in North Carolina which involves the modification of boat engines in such a way as to direct the propeller wash downwards instead of backwards. The propeller wash is sufficiently powerful in shallow water to suspend bottom sediments and clams into a plume in the water column, which allows *M. mercenaria* to be collected in a trawl net towed behind the boat (see Figure 2). To reproduce this process, we employed a commercial clam kicker and his boat. We measured in a crude way the relative intensity of the harvest treatment by counting all legally marketable (>2.54 cm in thickness in North Carolina) *M. mercenaria* removed and then estimating the percent removed of those available using the initial spring 1980 sampling (Table 2). We also recorded the number of

FIGURE 2.—Aerial photograph of a clam kicking boat in operation, showing the sediment plume in the wake and the tracks of previous kicking passes in the surrounding bottom.

TABLE 2.—The intensity of clam harvest treatments. All numbers and percents refer to legally harvested *Mercenaria mercenaria* >2.54 cm in thickness.

Habitat and harvest treatment	Treatment date and parameter estimated								
	May 1980			Winter 1980-81			Both applications pooled		
	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest	No. of clams removed	Est. % of spring 1980 clams removed	Effort required in harvest
Sand flat									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	191	16	170 min	140	11	210 min	331	27	380 min
Light-Kicking	140	17	2 passes 9 min	177	22	4 passes 30 min	317	39	6 passes 39 min
Intense-Kicking I	176	65	4 passes 20 min	165	61	3 passes 30 min	341	125	7 passes 50 min
Intense-Kicking II	384	47	8 passes 43 min	394	48	9 passes 87 min	778	95	17 passes 130 min
Seagrass bed									
Control I	0	0	0	0	0	0	0	0	0
Control II	0	0	0	0	0	0	0	0	0
Raking	134	1.9	275 min	925	13	2,125 min	1,059	15	2,400 min
Light-Kicking	91	1.4	2 passes 9 min	963	15	18 passes 121 min	1,054	16	20 passes 130 min
Intense-Kicking I	136	2.6	4 passes 22 min	2,608	49	32 passes 179 min	2,744	52	36 passes 201 min
Intense-Kicking II	1,033	12	12 passes 73 min	3,168	36	23 passes 156 min	4,201	48	35 passes 230 min

passes of the kicking boat and the minutes of clam kicking applied (Table 2). All *M. mercenaria* collected were returned to the laboratory for size-frequency estimates. The cumulative removals from the 2 clam harvesting applications produced relative treatment intensities acceptably close to our initial intentions (Table 2). For the hand raking treatment, we used short-handled rakes with 6-10 prongs of ≅14 cm in length separated by 3.5 cm gaps (see description and photograph of "pea digger" in Peterson et al. 1983a). We attempted to equalize the intensities of the raking and light-kicking treatments by removing equal percentages of the legally harvestable *M. mercenaria* from each of these two treatment matrices (Table 2). We also recorded the length of time actually spent raking as another indication of treatment intensity (Table 2).

RESULTS

Initial Sampling and Estimation of Shelliness

Within each habitat (sand flat and seagrass bed), one-way ANOVA was used on log $(x + 1)$-transformed data (which eliminated heteroscedacity in Cochran's tests) to assess whether any response variables differed significantly among the 6 matrices in spring 1980 prior to application of harvest treatments. There was no significant ($\alpha = 0.05$) initial variation among sand-flat matrices in any parameter: average total density of hard clams, average density of hard clam recruits (length <2.5 cm), average dry mass of seagrass, average density of all benthic macroinvertebrates, and sediment size (ϕ) (Table 3). Furthermore, the average percent organic content of sediments did not vary significantly among sand-flat matrices ($P > 0.05$ in ANOVA on angular-transformed proportions). Bay scallops were so rare in this initial sampling that we do not even record their densities in Table 3: bay scallops showed no significant difference among matrices in either habitat. The seagrass matrices exhibited significant initial variation in all parameters except average total density of hard clams and bay scallop density (Table 3). Variation in the other 4 parameters was not consistent across all seagrass matrices. A posteriori Duncan's tests, used to identify how specific seagrass matrices differed, show that the control II and raking matrices had significantly higher densities of hard clam recruits than all other seagrass matrices in spring 1980. Average seagrass biomass was significantly greater in intense-kicking I and significantly lower in control I than in all other seagrass matrices in the initial sampling. Control I also initially possessed a significantly higher average density of benthic macroinvertebrates, about 3 times the levels in the other seagrass matrices (Table 3). Duncan's test on mean ϕs revealed that in seagrass the raking and light-kicking matrices possessed

significantly higher initial ϕ values (finer sediments), although the differences among matrices were small. Percent organic content did not differ significantly ($P > 0.05$) among seagrass matrices in a one-way ANOVA on angular-transformed proportions.

The results of this initial sampling in spring 1980 prior to any application of clam harvest treatments imply that the sand-flat matrices were initially quite homogeneous. Consequently, any treatment effects can be expected to appear as significant differences that emerge among matrices in some or all samplings after application of the treatments. However, the initial differences among seagrass matrices imply that treatment effects may not be so readily identified. For those variables that exhibited initial differences among matrices, we performed two different tests of the effects of treatment. We performed simple ANOVA's to test for differences following treatment and we also, by subtraction of matrix means for spring 1980, adjusted the data from each matrix for initial differences and tested by ANOVA for significant changes in the differences among matrices. The first approach is appropriate if one believes that initial differences among matrices do not reflect intrinsic between-matrix differences that require adjustment, whereas the second approach assumes that initial differences among matrices would be expected to persist or recur in the absence of any treatment. An examination of how replicate matrices vary over time helps resolve which test procedure is more appropriate, but we performed both tests to provide a more robust set of conclusions.

Although all matrices in each habitat were chosen to be homogeneous in surface appearance, our October 1985 estimates of coarse shelliness of the surface (0-12 cm) sediments demonstrated that seagrass control I had almost 10 times the amount of coarse shell than any of the other seagrass matrices. The average ($\pm$SE) mass of shell fragments >3 mm in the top 12 cm of the 0.25 m^2 area in seagrass control I was 5,257 g ($\pm$701) compared with a range of 375 ($\pm$70) to 777 ($\pm$135) g across the other 5 seagrass matrices. This substantially larger amount of shell ($P < 0.001$ in a one-way ANOVA) seemed to be present during the entire experiment. Because surface shell fragments could greatly influence seagrass growth and especially *M. mercenaria* recruitment and survival (see Castagna and Kraeuter 1977), this physical anomaly of seagrass control I renders it a questionable control for the various treatment matrices. Similar data on surface shelliness taken from the sand matrices in October 1985 revealed no significant differences ($P > 0.05$) among matrices in a one-way ANOVA, with mean ($\pm$SE)

TABLE 3.—Contrasts among replicate matrices within each habitat before application of harvest treatments. Data are sample means ($\pm$SE) from spring 1980 (22 Feb.-6 May). Sample sizes appear in Table 1. Superscripts A and B indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly. Where ANOVA was nonsignificant, no means differ significantly.

	Habitat and sample average for each paramenter									
	Sand flat					Seagrass bed				
Future matrix designation	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic invertebrates per 0.008 m^2	Graphic mean sediment size (ϕ)	Total hard clam density per ¼ m^2	Density of hard clam recruits[1] per ¼ m^2	Seagrass dry mass (g per ¼ m^2)	Density of benthic invertebrates per 0.008 m^2	Graphic mean sediment size (ϕ)
Control I	0.50 (0.14)	0.22 (0.10)	0.00	6.00 (1.34)	2.14 (0.00)	2.42 (0.44)	0.17^{B} (0.06)	10.36^{C} (2.38)	16.50^{A} (4.32)	2.75^{B} (0.21)
Control II	0.33 (0.10)	0.17 (0.07)	0.00	4.67 (0.76)	2.16 (0.03)	2.28 (1.72)	0.81^{A} (0.16)	14.37^{B} (2.23)	4.33^{B} (0.88)	2.94^{B} (0.12)
Raking	0.47 (0.13)	0.17 (0.06)	0.00	4.67 (0.84)	2.17 (0.04)	2.19 (0.38)	$0.53^{A,B}$ (0.14)	16.01^{B} (3.49)	4.83^{B} (1.11)	3.38^{A} (0.07)
Light-Kicking	0.25 (0.09)	0.06 (0.04)	0.00	6.00 (1.26)	2.16 (0.02)	2.28 (0.33)	0.39^{B} (0.11)	19.56^{B} (2.62)	5.67^{B} (2.08)	3.46^{A} (0.07)
Intense-Kicking I	0.36 (0.14)	0.17 (0.07)	0.00	3.17 (0.83)	2.10 (0.02)	1.83 (0.28)	0.39^{B} (0.10)	41.22^{A} (4.03)	6.50^{B} (1.52)	2.84^{B} (0.15)
Intense-Kicking II	0.47 (0.14)	0.17 (0.07)	0.00	5.67 (1.38)	2.18 (0.01)	2.56 (0.36)	0.27^{B} (0.09)	28.44^{B} (4.17)	5.67^{B} (2.33)	2.69^{B} (0.05)
Statistical significance[2]	NS	NS	NS	NS	NS	NS	***	***	*	**

[1]Recruits defined as <2.5 cm in length (see Peterson et al. 1983b for size data on 0 year class as support).
[2]* - $P < 0.05$, ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA comparing matrices before experimental initiation.

mass of shell fragments >3 mm ranging from 28 (±7) to 157 (±121) across the 6 sand-flat matrices.

Our field plots were closed to all commercial and recreational shellfishing during the 4 years of the experiment by proclamation of the North Carolina Division of Marine Fisheries to avoid disruption of the experiments. However, on 7 occasions out of 50 days of observation, we observed clammers within the boundaries of our plots: 5 times in seagrass control matrix I and once in both the seagrass raking matrix and the intense-kicking II matrix. This represents significantly more illegal clamming in control I than would be expected by chance alone ($P < 0.01$ in a binomial test). Thus, the seagrass control I matrix may not represent a true control for our experiment.

Posttreatment Sampling

Mercenaria mercenaria Recruitment

In the sand-flat habitat there were only two Octobers during which *M. mercenaria* recruits were sampled: October 1980 after the initial application of the clam harvest treatments and October 1981 after both treatment applications. In neither sampling did a one-way ANOVA on log (x + 1)-transformed counts (which removed heteroscedacity in Cochran's tests) reveal significant ($\alpha = 0.05$) variation in average density of recruits among sand-flat matrices (Table 4). Furthermore, a two-way ANOVA on log (x + 1)-transformed counts from both time periods, done to increase the power of the test of matrix differences, also failed to reveal any significant variation in average recruitment among sand-flat matrices. Despite the failure to demonstrate statistical significance in *M. mercenaria* recruitment among sand-flat matrices, the average density of recruits in the control matrices during these two Octobers was more than double (on untransformed scale) the average density in the 2 high-intensity clam kicking matrices (Fig. 3). Some of this difference may have been present even before treatments were applied (Fig. 3), but it is also possible that the high local variability in recruitment lowers the power of this test of harvest treatment to a degree that even a twofold difference is undetectable.

During 4 Octobers, *M. mercenaria* recruitment was estimated in the seagrass habitat (Table 4). One of these, October 1980, fell after the first harvest treatment (which Table 2 shows to have been very light in the seagrass plots) but before the second, more intense treatment. The other 3 samplings came in successive years, increasingly far from the actual time of application of the harvest treatments. Because of the preexisting significant differences

TABLE 4.—The impact of clam harvesting on recruitment of *Mercenaria mercenaria*. Entries are mean numbers (± SE) of recruits per ¼ m^2. Recruits are defined as all individuals <2.5 cm in length in October of each year. For 1980 and 1981, n = 36 samples from each treatment matrix in each habitat, whereas for 1982 and 1983, n = 9 for seagrass and 0 for sand flat.

	Habitat and date							
	Sand flat			Seagrass bed				
Treatment matrix	1980	1981	Unweighted average	1980	1981	1982	1983	Unweighted average
Control I	0.33 (0.11)	0.17 (0.06)	0.25	0.94 (0.21)	0.61^{A} (0.13)	$0.67^{A,B}$ (0.24)	0.67 (0.24)	0.72
Control II	0.36 (0.11)	0.06 (0.04)	0.21	0.72 (0.15)	0.28^{B} (0.09)	$1.33^{A,B}$ (0.47)	1.56 (0.77)	0.97
Raking	0.44 (0.13)	0.14 (0.08)	0.29	0.81 (0.14)	0.22^{B} (0.07)	$0.78^{A,B}$ (0.32)	1.67 (0.55)	0.87
Light-Kicking	0.19 (0.08)	0.08 (0.05)	0.14	0.61 (0.13)	0.11^{B} (0.05)	2.11^{A} (0.68)	0.33 (0.17)	0.79
Intense-Kicking I	0.11 (0.05)	0.03 (0.03)	0.07	0.42 (0.11)	$0.39^{A,B}$ (0.10)	0.22^{B} (0.15)	0.67 (0.17)	0.43
Intense-Kicking II	0.22 (0.07)	0.08 (0.05)	0.15	0.56 (0.14)	$0.33^{A,B}$ (0.10)	0.56^{B} (0.24)	0.33 (0.24)	0.45
Statistical significance[1]	NS	NS	NS	NS	**	*	NS	*

[1] * - $P < 0.05$, ** - $P < 0.01$ in one-way ANOVA's on each date and two-way ANOVA's over all dates, reported in the unweighted average column. These analyses were performed on log-transformed data, which eliminated or reduced heteroscedacity in Cochran's tests. Superscripts A and B indicate significant differences in Duncan's test at $\alpha = 0.05$. No Duncan's test results are given for the unweighted averages in the seagrass bed because the two-way ANOVA exhibited highly significant ($P < 0.001$) interaction between date and treatment.

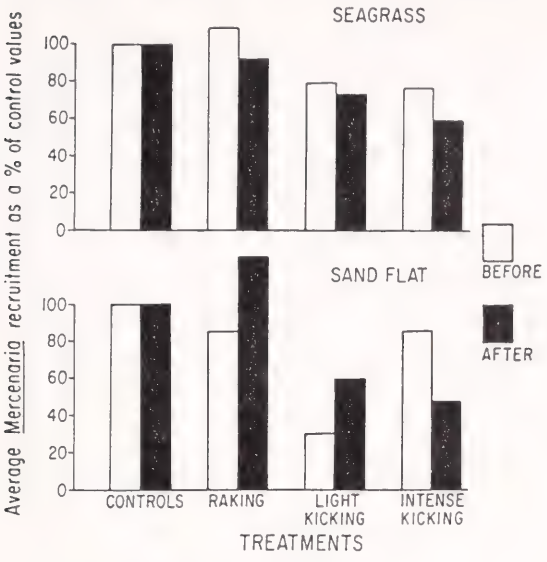

FIGURE 3.—Average density of *Mercenaria* recruits (<2.5 cm in length) before harvest treatments in spring 1980 and after in October 1980 and 1981 (averaged together). ANOVA's showed no significant effect in the sand flat but several significant changes after treatment in the seagrass bed (see Table 4). Seagrass matrices are grouped together for illustration of effects on the basis of results of Duncan's tests performed on 1980 and 1981 data adjusted for spring 1980 differences in recruit densities. Consequently, these groupings separate those seagrass matrices that changed in recruitment pattern after treatment.

among seagrass matrices in *M. mercenaria* recruitment, we analyzed the posttreatment data by both simple ANOVA to test for differences in each postharvest sampling and by ANOVA on adjusted data to test for significant changes away from the initial differences. The results of these two different sorts of analysis were inconsistent. ANOVA's on simple recruit densities [log $(x + 1)$-transformed, which homogenized variances in Cochran's tests] demonstrated significant differences among matrices in October 1981 and 1982, but not in 1980 or 1983. Duncan's tests on the 1981 and 1982 results showed few significant differences and no consistent difference in these 2 years (Table 4). The unweighted means suggest that *M. mercenaria* recruitment may have been less in the 2 intensely kicked matrices, but the two-way ANOVA had a significant date by treatment interaction preventing application of Duncan's test.

Despite an indication of lower *M. mercenaria* recruitment in the 2 intensely kicked matrices (Table 4), ANOVA's performed on recruit data adjusted for initial differences among matrices to test whether those differences changed after treatment revealed a different pattern. Only the 1980 and 1981 results were significant (both at $P < 0.001$). The patterns of change in recruitment among matrices were the same in Duncan's tests on both 1980 and 1981 data (Fig. 3). The shelly control I exhibited over 4 times as much recruitment in October 1980 and 1981 as in spring 1980, while control II exhibited about a 40% decrease after harvest (Fig. 3). Raking and light-kicking matrices behaved similarly, showing about the same value after harvest as before. The 2 intense-kicking matrices showed about a 30% increase in *M. mercenaria* recruitment after harvest (Fig. 3). Thus, the ANOVA's on adjusted data produce results dependent upon whether control I is discarded or averaged together with control II.

This demonstrates that conclusions about how clam harvest affects *M. mercenaria* recruitment are not robust to the decision of how to treat the shelly control or to the relaxation of the assumption that matrices are expected to repeat any initial differences in recruitment in the absence of treatment as an intrinsic characteristic. The choice of analysis might be made by examining whether matrices that are treated identically show similar or dissimilar patterns of recruitment in different years. A comparison of all posttreatment recruit data in the 2 intensely kicked matrices (Table 4) reveals that they never differed from one another significantly, although the mean difference and even ranking between them varied. The 2 control matrices diverged radically from one another (Table 4), but unpredictable illegal clamming in matrix I may be at least partly responsible. Because of the ambiguities in these data, it is impossible to draw any firm conclusion on how treatments affected *M. mercenaria* recruitment in the seagrass.

Seagrass Biomass

Because of substantial and significant differences among seagrass matrices in seagrass biomass in spring 1980 before application of any treatment, we analyzed the posttreatment data by both simple ANOVA to identify significant differences among matrices after treatment and also by ANOVA on adjusted observations to test for significant change in the initial pattern of biomass differences among matrices. The results of these 2 types of analysis are qualitatively identical, so we present only the results on adjusted data. We prefer this analysis because the *Zostera marina* and *Halodule wrightii* in North Carolina are perenials that do not readily and quickly spread into new areas (Thayer et al. 1985), so that initial patterns of difference in seagrass biomass

might be expected to persist in the absence of treatment effects. All ANOVA's were performed on untransformed data (seagrass biomass or differences in seagrass biomass) because Cochran's test for heteroscedacity was nonsignificant on 2 of the 6 data sets and log and square root transformations failed to reduce the significance level ($P < 0.05$ on 2 and $P < 0.01$ on the other 2).

There was a clear and large effect of intense kicking. The ANOVA's on adjusted data were highly significant for every posttreatment sampling date, indicating that the initial differences among seagrass matrices in average seagrass biomass shifted significantly after application of harvest treatment and never returned to initial levels even by fall 1984. The 2 intense-kicking treatments had consistently low seagrass even after the first light treatment but especially after both treatment applications. Light kicking and raking never differed significantly from one another in seagrass biomass. The shelly control I matrix diverged from the other control (II) in having low values in all posttreatment samplings, often grouping with the 2 intense-kicking matrices in the Duncan's test (Table 5).

Average biomass of seagrass in each treatment matrix is compared in Figure 4 to the changes that would be predicted from the average biomass in the 2 untreated control matrices. This approach smoothes out the seasonality and other temporal variability by normalizing all the treatment means to the control values. It assumes that the differences among matrices observed in spring 1980 in average biomass would be expected to persist indefinitely and then calculates what percent of the expected seagrass biomass each treatment matrix actually exhibited on each sampling date. This assumption is clearly violated by the divergent behavior of the 2 control matrices, but it provides a conservative estimate of the effects of harvest because the average of the 2 controls includes control matrix I, which exhibited low seagrass biomass, perhaps because of enhanced illegal clamming. Clam harvest treatments immediately reduced seagrass biomass below the expected amounts, with greater effects of the second, more intense (see Table 2), harvest treatments. The 2 intense clam-kicking treatments exhibited a decline of about 65% in expected biomass from spring 1980 until spring 1981, while biomass declined by about 25% below expected in the raking and light-kicking matrices. Seagrass biomass recovered to equal and even exceed expected values by the very next sampling period in fall 1981 in the raking and light-kicking matrices, and remained high for the next 3 years. However, recovery in seagrass biomass in the 2 intense-kicking matrices did not begin to occur until sometime in fall 1982-fall 1983 (Fig. 4) and was not yet complete by fall 1984. In fall 1984, almost 4 years after the second harvest treatment, average biomass of seagrass in the 2 intense-kicking plots was only 65% of the expected levels. These estimates are conservative if the shelly control (I) matrix is actually a poor control for this experiment because we used the mean of both controls as an expected value for Figure 4. Scheffé a priori contrasts of matrix means (in Table 5) show that, despite the divergence of the 2 controls, the mean seagrass biomass was significantly ($P > 0.05$) less in the 2 intense-kicking matrices than expected from the 2 controls in all sampling periods after application of both harvest treatments. This test provides the statistical justification for our presentation of differences in Figure 4.

TABLE 5.—The impact of clam harvesting on the average seagrass dry mass (± SE) per ¼ m^2 within the seagrass habitat. Data presented for each date and matrix are the mean (± SE) dry mass of seagrass per sample minus the mean dry mass in spring 1980 for that particular matrix (from Table 3). Sample sizes appear in Table 1. Clam harvesting treatments occurred between spring 1980 and fall 1980 and again between fall 1980 and spring 1981. Superscripts A-D indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrices	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Fall 1984
Control I	2.2(2.9)^{C,D}	19.5(11.2)^{A}	7.4(3.3)^{B}	11.9(6.1)^{A}	1.2(4.4)^{B}	8.0(7.2)^{B}
Control II	19.7(2.7)^{A}	25.8(4.0)^{A}	20.0(2.0)^{A}	22.8(5.2)^{A}	40.1(5.9)^{A}	40.8(3.8)^{A}
Raking	7.7(1.8)^{B,C}	10.5(3.2)^{A}	15.2(2.0)^{A,B}	13.6(5.1)^{A}	38.2(7.0)^{A}	41.1(5.4)^{A}
Light-Kicking	13.8(2.9)^{A,B}	14.4(6.0)^{A}	15.3(3.0)^{A,B}	13.6(3.5)^{A}	31.9(4.7)^{A}	35.7(5.1)^{A}
Intense-Kicking I	−1.5(2.7)^{D}	−21.2(6.9)^{B}	−18.8(4.3)^{C}	−29.0(6.1)^{C}	−18.8(6.0)^{C}	5.6(9.1)^{B}
Intense-Kicking II	7.1(3.7)^{B,C}	−9.1(5.4)^{B}	−12.2(3.1)^{C}	−11.3(7.2)^{B}	9.2(10.8)^{B}	1.5(4.4)^{B}
Statistical significance[1]	***	***	***	***	***	***

[1] *** - $P < 0.001$ in one-way ANOVA's on untransformed dry masses, comparing the matrix means on each separate date. ANOVA's were performed on the differences from spring 1980 matrix means because of pre-existing significant differences among matrices in spring 1980 before application of harvest treatments.

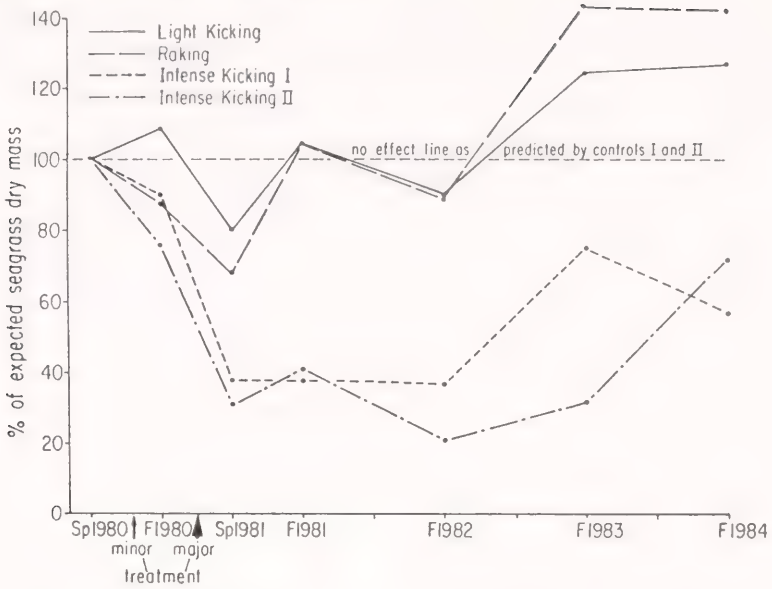

FIGURE 4.—Percent difference between observed average biomass of seagrass in each treatment matrix and expected biomass based on the assumption that initial differences between the two control matrices and each treatment matrix would be expected to remain constant across time. The expected biomass is then plotted as 100% (the no effect line). Times of the two clam harvest treatments are indicated with arrows on the x-axis.

Benthic Macroinvertebrates

In the sand-flat habitat, the average density of benthic macroinvertebrates never varied significantly among matrices (Table 6) in any of the 3 posttreatment sampling dates [one-way ANOVA's were run on log $(x + 1)$-transformed counts, using a separate analysis for each date]. The sums over all 3 posttreatment dates of the average macroinvertebrate densities per core are nearly identical for each sand-flat matrix and a two-way ANOVA on log $(x + 1)$-transformed densities from all 3 time periods revealed no significant difference among matrices.

In the seagrass habitat, analogous one-way ANOVA's done separately for each date, demonstrated that the average density of benthic macroinvertebrates did not differ significantly among seagrass matrices in fall 1980 or spring 1981 (Table 6). A significant difference among matrices did appear in fall 1981, and in a two-way ANOVA on all 3 posttreatment dates together. Despite the statistical significance of 2 of 4 ANOVA's, actual differences in mean densities among seagrass matrices were proportionately small. Furthermore, Duncan's tests revealed a pattern of differences among matrices (Table 6) that was identical to the initial pattern of significant differences in the spring 1980 sampling before treatment (see Table 3).

Although the sums of the sample means from each of the 3 posttreatment sampling dates (Table 6) imply that benthic macroinvertebrate densities in the seagrass habitat were about double those in the sand flat, this pattern was not consistent across seasons. Nested ANOVA's, done on log $(x + 1)$-transformed counts and performed separately for each sampling date, showed that there was no significant difference between habitats during either spring sampling period (spring 1980 or 1981), whereas average densities of benthic macroinvertebrates were significantly greater ($P < 0.001$ in fall 1980 and $P < 0.005$ in fall 1981) in the seagrass habitat in both of the Octobers.

Although the clam harvesting treatments did not affect total density of benthic macroinvertebrates in either habitat, species composition might still have been altered. We identified all individuals in 16 cores in each habitat from the spring 1980 pretreatment sampling (4 cores randomly chosen from each control matrix and from each intense-kicking matrix) and in 16 cores in each habitat from the spring 1981 posttreatment sampling (drawn equally from each of the same matrices). This comparison holds season constant and permits us to test for any gross shifts

TABLE 6.—The impact of clam harvesting on average density (± SE) of benthic macroinvertebrates per 0.008 m^2. n = 6 samples for each treatment matrix at each sampling date. Samples were taken to 25 cm and passed through 1 mm mesh. Superscripts A-C indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

	Habitat and date							
	Sand flat				Seagrass bed			
Treatment matrix	Fall 1980	Spring 1981	Fall 1981	Sum	Fall 1980	Spring 1981	Fall 1981	Sum
Control I	8.0 (2.7)	5.7 (1.2)	8.0 (1.4)	21.7	34.3 (7.8)	9.3 (1.8)	16.2^{A} (2.9)	59.8^{A}
Control II	11.7 (1.5)	7.7 (1.4)	4.2 (0.8)	23.6	19.0 (2.0)	10.5 (1.6)	$11.0^{A,B}$ (1.6)	40.5^{B}
Raking	6.5 (0.5)	8.2 (1.0)	4.8 (0.8)	19.5	39.8 (5.1)	6.8 (1.1)	$12.0^{A,B}$ (2.4)	58.6^{B}
Light-Kicking	12.3 (2.6)	11.5 (3.0)	4.5 (0.9)	28.3	29.5 (8.6)	5.8 (1.3)	$7.8^{B,C}$ (1.3)	44.1^{B}
Intense-Kicking I	7.8 (0.7)	8.7 (1.7)	6.3 (1.4)	22.8	23.5 (4.8)	8.7 (2.9)	6.5^{C} (1.2)	38.7^{B}
Intense-Kicking II	9.7 (2.2)	6.0 (1.3)	5.0 (0.8)	20.7	34.5 (10.7)	6.3 (1.1)	6.0^{C} (0.9)	46.8^{B}
Statistical significance[1]	NS	NS	NS	NS	NS	NS	**	***

[1] ** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA's (for each separate date) and two-way ANOVA's (for sums) on average macroinvertebrate counts per core (transformed by log $(x + 1)$).

in species composition as a function of the intense-kicking treatment. Table 7 presents the results of these species identifications and shows that no major shift in species composition of the most abundant species occurred in either the sand-flat or seagrass habitat following the application of the intense-kicking treatment. Polychaetes dominated the fauna of both habitats and the same species of polychaetes tended to be represented at similar densities both before and after intense clam kicking.

Bay Scallop Densities

Bay scallops were never encountered in sampling the sand-flat matrices, so we have no test of whether clam harvest treatment affects bay scallops in areas lacking seagrass. One-way ANOVA's on log $(x + 1)$-transformed counts (which removed heteroscedacity in Cochran's tests) demonstrated significant ($\alpha = 0.05$) differences among seagrass matrices in average bay scallop density on only 2 sampling dates, fall 1980 and fall 1983 (Table 8). Duncan's test on the fall 1980 data showed that bay scallop density in control I was significantly ($P < 0.05$) lower than in every other matrix except intense-kicking II, and that there were no other significant differences between pairs of matrices. Because the fall 1980 sampling occurred before the major application of clam harvest treatments (see Table 2), this sampling period may be considered a pretreatment sampling. Extremely low seagrass biomass in control I in fall 1980 (Table 5) may explain the significantly lower bay scallop densities in that matrix on that date.

The fall 1983 sampling occurred after a period of more successful bay scallop recruitment than occurred before any other sampling date (Table 8) and, thus, provided more "substrate" on which effects of clam harvest treatments may have operated. Duncan's test on mean bay scallop densities for fall 1983 demonstrated that the matrices split into two separate groups: a low-density group, made up of control I and the 2 intense-kicking matrices, and a high-density group, comprised of control II, the raking, and light-kicking matrices (Table 8). Within each group, no matrices differed significantly ($\alpha = 0.05$) from any other, but all differences between groups were statistically significant. Because fall 1983 bay scallop densities were so much greater than at any other sampling date, the sums over all five sampling periods also exhibited significant differences among matrices in an analogous two-way ANOVA, and Duncan's tests separated the matrices into groupings virtually identical to those detected for the fall 1983 data set alone (Table 8).

A contrast of the bay scallop results of fall 1980 and fall 1983 demonstrates that after application of the second intense-kicking treatment in the seagrass habitat in winter of 1980-81, bay scallop densities declined to join the already low value of control I,

which together formed a group of low-density bay scallop matrices. About 84% of the variance in bay scallop densities in fall 1983 is explained by seagrass biomass in a simple linear regression. Figure 5 presents the relationship between average seagrass biomass and bay scallop densities on a 1,225 m^2 scale, which suggests that the 2 intense-kicking matrices contained even fewer bay scallops than predicted from their reduced seagrass biomass. This is similarly illustrated from calculations of the mean numbers of bay scallops per 100 g of seagrass in each matrix in fall 1983: control I (5.7), control II (5.1), raking (4.7), light kicking (4.3), intense-kicking I (2.0), and intense-kicking II (2.3).

TABLE 7.—For each habitat, total numbers of individuals found in four randomly chosen cores from each of the two controls and the two intense-kicking matrices on two dates, one before and one after clam-harvest treatment. All species with total counts greater than two are listed separately.

	Spring 1980 Before treatment		Spring 1981 After treatment	
Species	Controls	Intense-kicking	Controls	Intense-kicking
Sand-flat habitat				
Aricidia fragilis	7	1	6	5
Notomastus hemipodus	3	4	5	5
Platynereis dumerilii	1	0	5	7
Axiothella sp.	3	2	1	7
Drilonereis magna	5	5	0	1
Spiochaetopterus oculata	0	2	3	3
Arabella iricolor	3	1	1	2
Glycera sp.	5	1	0	0
Others[1]	5	2	2	1
Seagrass habitat				
Axiothella sp.	23	8	7	4
Platynereis dumerilii	12	8	14	1
Notomastus hemipodus	20	7	4	0
Tharynx marioni	3	4	3	2
Nereis falsa	0	1	5	5
Glycera sp.	3	4	2	1
Melinna maculata	1	0	6	3
Onuphis jenneri	0	1	3	3
Lumbrinereis sp.	0	0	4	3
Spiochaetopterus oculata	1	0	4	0
Spionidae	4	0	0	1
Sthenelais limicola	0	1	1	1
Arabella iricolor	0	2	1	0
Poecilochaetus sp.	3	0	0	0
Onuphidae	0	0	3	0
Others[1]	1	2	1	1

[1]These include molluscs, an amphipod, and additional polychaetes.

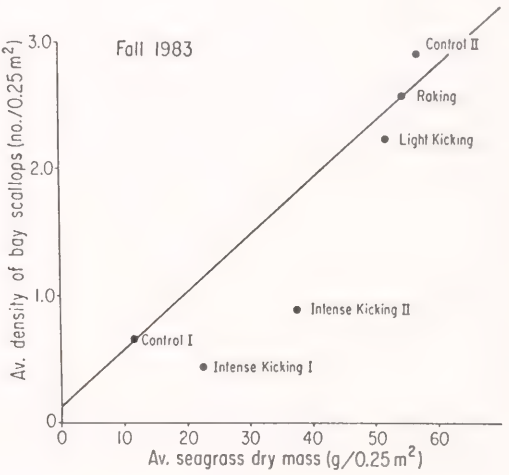

FIGURE 5.—Relationship between the average density of bay scallops, *Argopecten irradians*, and the average biomass of seagrass in fall 1983 samplings of each control and treatment matrix of the clam harvest experiment in the seagrass matrix. Clam harvest treatments had been applied in spring 1980 and again in winter 1980-81.

TABLE 8.—The effect of clam harvesting in the seagrass habitat on average bay scallop, *Argopecten irradians*, density per ¼ m^2 (± SE). Sample sizes per treatment matrix were 36 in fall 1980 and fall 1981 and 9 in spring 1981, fall 1982, and fall 1983. No data are presented for the sand flat because of the rarity of bay scallops in that habitat. Superscripts A-C indicate significant differences among matrices in Duncan's test at $\alpha = 0.05$, with those means sharing capital letter superscripts not differing significantly.

Treatment matrix	Sampling date					
	Fall 1980	Spring 1981	Fall 1981	Fall 1982	Fall 1983	Sum
Control I	$0.11(\pm 0.05)^{B}$	$0.44(\pm 0.24)$	$0.05(\pm 0.04)$	$0.11(\pm 0.16)$	$0.66(\pm 0.33)^{B}$	1.37^{C}
Control II	$0.63(\pm 0.11)^{A}$	$1.00(\pm 0.37)$	$0.14(\pm 0.07)$	$0.22(\pm 0.15)$	$2.89(\pm 0.51)^{A}$	4.88^{A}
Raking	$0.53(\pm 0.14)^{A}$	$0.78(\pm 0.28)$	$0.16(\pm 0.06)$	$0.44(\pm 0.24)$	$2.56(\pm 0.67)^{A}$	4.47^{A}
Light-Kicking	$0.75(\pm 0.18)^{A}$	$0.33(\pm 0.33)$	$0.14(\pm 0.07)$	$0.89(\pm 0.42)$	$2.22(\pm 0.46)^{A}$	4.33^{A}
Intense-Kicking I	$0.50(\pm 0.12)^{A}$	$0.22(\pm 0.15)$	$0.03(\pm 0.03)$	$0.00(\pm 0.00)$	$0.44(\pm 0.29)^{B}$	$1.19^{B,C}$
Intense-Kicking II	$0.39(\pm 0.11)^{A,B}$	$0.56(\pm 0.18)$	$0.14(\pm 0.07)$	$0.55(\pm 0.24)$	$0.88(\pm 0.35)^{B}$	2.52^{B}
Statistical significance[1]	**	NS	NS	NS	***	***

[1]** - $P < 0.01$, *** - $P < 0.001$, NS - $P > 0.05$ in one-way ANOVA on log $(x + 1)$-transformed sample counts, comparing matrix means on each date and in a two-way ANOVA over all dates (in the sums column).

DISCUSSION

The one-way ANOVA's which we performed to test the significance of differences in parameter means among matrices at any given sampling date can demonstrate heterogeneity among matrices. If there is no significant heterogeneity, we probably can conclude safely that there was no effect of treatment on that parameter at that sampling date, assuming that equivalent levels of the parameter prevailed before application of the treatment (which was not always true). If, on the other hand, the one-way ANOVA demonstrates significant differences among matrices, this result does not necessarily imply that the treatment was the cause. Replication in these ANOVA's is generated from subsamples within each individual matrix. These subsamples taken from within a given matrix are not independent because of their spatial proximity. Consequently, matrices can diverge in various ways from one another over the course of an experiment, caused by extraneous events that act on the scale of the plot (matrix) to destroy independence among subsamples. This experimental design would be termed pseudoreplication (Hurlbert 1984), and permits a test of whether plots differ significantly and does not allow an unambiguous assignment of observed differences to the treatment applied (but see Stewart-Oaten et al. 1986). For that reason, we replicated both our control matrices and our intense-kicking matrices in each habitat. These permit us to use a priori contrasts, with replication of 2 separate, independent plots, to test unambiguously whether the most important treatment (intense clam kicking) was responsible for observed changes. Appreciation of the differences between these two sorts of analyses is necessary to interpret properly the results of this study.

Although we designate our heavier clam-kicking treatment "intense", it probably falls well short of the effort that commercial clammers would apply to a productive seagrass bottom; we took only an estimated 50% of the clams legally available for harvest (Table 2). Consequently, the intensity of harvest that we applied in the seagrass is not unreasonably high. In the sand-flat system, we took approximately 100% of the estimated numbers of legally available clams in our intense treatments. Although higher than the percent taken in the seagrass, this probably better approximates the fishing intensity that is applied to productive unvegetated areas by commercial clammers. Efficiency of returns remained high even in the high-intensity kicking matrices, as compared with hand raking. In the sand flat, light kicking produced an average of 8.1 clams per minute and intense kicking 6.2 clams per minute, compared with a return of only 0.9 clams per minute from hand raking (Table 2). In the seagrass bed, light kicking yielded an average of 8.1 clams per minute and intense kicking 16.1 clams per minute, in contrast to a return of only 0.4 clams per minute from hand raking (Table 2). Thus, efficiency of harvest, defined as clams caught per unit of time, was clearly greater by over an order of magnitude with the mechanical technique than with the traditional hand method. The improved efficiency during clam kicking in the seagrass as harvest intensity increased from taking about 15% to about 50% of available clams is probably caused by the gradual removal of seagrasses which, when present, reduce the efficiency of clamming.

To test whether hard clam harvest affects its own recruitment in the area of harvest, we counted new recruits (<2.5 cm in length, Peterson et al. 1983b). Recruitment, when estimated in this fashion, confounds both larval (and postlarval) settlement with subsequent early mortality from time of settlement until October. Consequently, we do not directly test the hypothesis that natural densities of adult hard clams inhibit larval settlement in their vicinity. Furthermore, our clam harvest treatment not only removes many larger hard clams, but it also disturbs the bottom sediments. Consequently, there are several plausible mechanisms by which our clam harvest treatments may affect October recruitment of hard clams: 1) reduction of adult hard clam density may affect hard clam settlement (positively, if negative adult-larval interactions predominate, as suggested by most past studies: Woodin 1976; Williams 1981; Peterson 1982b) or survivorship from settlement until October (no a priori prediction from the literature on what direction this effect may take), or 2) disturbance of the bottom may alter hard clam settlement (positively, if hard clam larvae select disturbed sediments, which seems unlikely, or negatively if hard clam larvae avoid disturbed sediments) or early survivorship (negatively, if the clam harvest buries small clams too deeply to reemerge or if disturbance has removed protective seagrass or shell materials and thereby made juvenile hard clams more vulnerable to predators (Peterson 1982a; Summerson and Peterson 1984)).

Our data on hard clam recruitment are sufficiently ambiguous to preclude any definitive answers to the question of how clam harvest affects subsequent recruitment. In the sand flat, there was no significant effect of harvest treatment, but the 2 intensely kicked matrices yielded only 50% of the recruits

produced by the 2 controls (Fig. 3). In the seagrass, *M. mercenaria* recruitment may also have been reduced by harvest treatments (Table 4), but the conclusion depends upon the assumption that the shelly control I was an adequate control for recruitment data. Given the enhanced survivorship of *M. mercenaria* recruits in shell (Castagna and Kraeuter 1977) and the significant illegal clamming in seagrass control I, this assumption is questionable.

It is possible that removal of adult hard clams enhances larval settlement over a larger spatial scale than the 1,225 m^2 experimental plots because depletion of larvae by feeding from the water column should extend over a larger spatial scale (Peterson 1982b). Although it is possible that our sampling was on too fine a scale to detect such an effect, our sampling occurred on a far larger spatial scale by 3 orders of magnitude than any previous experimental test of adult-larval interactions and, thus, should have provided for greater opportunity to detect any positive effect of adult hard clam removal. The failure to demonstrate a response in the sand flat may be a different consequence of scale. Newly recruited hard clams may settle more heavily where adult densities have been reduced but the effect may be diffused away by the physical dispersal of new recruits by tidal currents and waves. As a consequence of such multiple interpretations, we can best conclude that on the scale of our experiments no dramatic increase in hard clam recruitment occurs with intense mechanical harvest of adult hard clams in seagrass and harvest may even reduce recruitment in both unvegetated and vegetated areas.

The effect of various clam harvest treatments in the seagrass bed on seagrass biomass (Fig. 4) is the most obvious result of this study. Clam harvest of all types had an immediate impact in reducing the seagrass biomass. Reduction of seagrass increased with harvest intensity, as was demonstrated both by the enhanced effect of the second treatment application, which was much more intense than the first, and also by the larger effects of intense kicking as compared with the other treatments (Fig. 4). Although the seagrass biomass in the raking and light-kicking matrices recovered to levels predicted from the controls within a year's time, the seagrass biomass in the intense-kicking matrices did not even begin to recover for 2 years and had not fully returned to predicted, control levels after 4 years. These results imply that if sufficient seagrass is destroyed, recovery is slow. Because our intense-kicking treatment removed only an estimated 50% of available hard clams and because the efficiency of hard clam capture per unit time of harvest was greater in the intense treatment than in the light treatment in the seagrass habitat, we suspect that commercial clam kickers would apply even more harvest intensity than we did in the this intense-kicking treatment. Consequently, the effects of commercial clam kicking in seagrass beds are probably underestimated by our data (Fig. 4). Furthermore, by using both control matrices (including the shelly one) in estimating the effects of harvest on seagrass biomass, we intentionally provide an additional conservative bias. Clam kicking at a low level (≅15% of available hard clams harvested) does not appear to be any more destructive of seagrass than hand raking that same number of clams, but the lack of replication of these two types of treatment matrices renders this a tentative conclusion.

The extremely slow recovery of seagrass in the intensely kicked seagrass matrices raises the possibility that seagrass beds and unvegetated sand flats may exist as alternative stable states (Sutherland 1974; Connell and Sousa 1983; Peterson 1984) on many of the same shallow bottoms of sounds and coastal lagoons. That is, a given shallow bottom may exist as either a seagrass bed or an unvegetated sand flat, but whichever state it occupies it is likely to retain for a relatively long period of time. Transformation from one state to another may require some input of external energy. Because great changes in current regime and surface sediment character are associated with the presence and growth of seagrasses (Ginsburg and Lowenstam 1958; Orth 1977; Fonseca et al. 1983; Peterson et al. 1984; Eckman in press), it is reasonable to hypothesize that destruction of seagrass may result in sufficiently higher energy at that site that natural reestablishment could be difficult. Certainly, the slow return of seagrass following intense clam kicking in our experiments implies that seagrass recovery even in previously vegetated areas is tenuous. If seagrass beds and unvegetated bottoms do tend to represent alternative stable states for large areas of the estuarine and sound bottom, then denuding of vegetation would have long-lasting effects, even beyond what we have demonstrated. Furthermore, transplantation of relatively dense seagrass may be necessary to produce rapid reversion back into a vegetated system (for reviews of disturbance, recovery, and transplantation of seagrasses see Zieman 1982; Thayer et al. 1985). Because of the important roles that seagrasses play in promoting estuarine productivity and coastal fisheries (Thayer et al. 1975), intense clam kicking in vegetated areas could have long-lasting and

serious impacts on many commercially important fisheries. Our own data imply a potentially negative impact on hard clam recruitment (Table 4) and a clear reduction in bay scallop abundance (Table 8) in part because of reduction in seagrass biomass.

Clam harvesting had no detectable effect on the abundance of small benthic invertebrates. The density data did not even suggest an effect (Table 6) and the composition of the most abundant species did not change, even with intense clam kicking (Table 7). This lack of response is probably a consequence of the dominance of small polychaetes in these invertebrate data. Small polychaetes make up most of the total infaunal density and all of the most abundant species. Small polychaetes tend to exhibit rapid turnover, quick colonization and short life spans, relative to molluscs, echinoderms, and many other invertebrates; consequently, they may be expected to recover more rapidly after disturbance. The large seasonal variability in total macroinvertebrate density at our seagrass sites is a reflection of the short-term response times of this fauna, which is known to exhibit large seasonal fluctuations in density in North Carolina (Commito 1974).

Like several previous studies of the densities of benthic infauna (Kikuchi 1966; Warme 1971; Orth 1977; Reise 1977, 1978; Stoner 1980; Summerson and Peterson 1984), our data demonstrate higher densities inside the seagrass bed than on unvegetated bottoms in October. However, the difference in infaunal density between habitats appears to vary seasonally, as shown previously (Reise 1978; Stoner 1980). In spring, the two habitats had approximately equal densities of infauna. Because estuarine densities of epibenthic predators, both fishes (Adams 1976; Orth and Heck 1980) and crustaceans (Heck and Orth 1980), also vary seasonally such that our fall samplings occur after months of high density and our spring samplings after a low-density season for epibenthic consumers, these new observations provide further support for the hypothesis (see review of concepts in Kikuchi 1980; experimental evidence in Reise 1977; Orth 1977; Summerson and Peterson 1984) that seagrass provides a natural refuge from predation for infaunal invertebrates.

Intense clam kicking caused a substantial decline in the average density of bay scallops in the seagrass habitat (Table 8). Most of the variation among matrices in the total densities of bay scallops and in the fall 1983 densities, when numbers were high, could be readily explained by the variation among matrices in average seagrass biomass. Bay scallops recruit to seagrass blades where they remain attached by byssal threads for the first few months of life. In addition, adult bay scallops, which are mobile, tend to be found in seagrass beds, as our failure to encounter them in the sand-flat samples illustrates. Their feeding may be more efficient in the slower currents of the seagrass environment (Kirby-Smith 1972). Consequently, it is not surprising that reductions in bay scallop density accompanied the declines in average seagrass biomass in our experiments. However, the apparent effect (Fig. 5) of intense clam kicking that persists even after the seagrass biomass effect is removed was a surprise. Because the application of clam kicking is necessarily patchy (it forms a trail behind the path of the boat) and, thus, produces an increase in the patchiness of the vegetation (see standard errors in Table 5), we suspect that this residual effect of intense clam kicking is a reflection of that enhanced seagrass patchiness. We hypothesize that the average biomass of seagrass present in our plots is more attractive (in a broad sense) to bay scallops when it is more uniformly distributed over a given area than when it is clumped into more discrete patches at least on the 0.25 m^2 scale of our samples.

The implications of this study for the management of the hard clam fishery depend upon the specific values attributed to various factors. Our data show clearly the enhanced efficiency that the mechanical clam harvesting process known as clam kicking brings to the fisherman who adopts it instead of hand raking. Yet the enhanced efficiency may itself be a danger if the resource is thereby overfished beyond its capacity to sustain harvest. Our data on the negative impacts of clam harvest do not permit one method to be selected in preference to another except to the degree that hand raking might never reach the same harvest intensity and, therefore, might not cause the same magnitude of effects on seagrass beds and their fauna. Outside seagrass beds, clam kicking does not appear to have any serious negative impacts on other parameters of ecological value with the possible exception of hard clam recruitment. This effect is probably a necessary price to pay for the harvest of the adult, marketable clams. Inside seagrass beds, effects of clam kicking on seagrass biomass and bay scallop abundance are quite serious and long-lasting. Because seagrass contributes so substantially to the production of many coastal fisheries (Thayer et al. 1985), any regulation that might limit the intensity of clam fishing in that habitat would probably be beneficial. Restriction of the much more efficient mechanical clam harvesters to unvegetated bottoms may be a suitable mechanism for limiting the total harvest pressure in seagrass beds and, thereby, preserving other fish-

eries in the face of emerging new technology, which has the potential to enhance greatly the user conflicts for limited and interdependent coastal and estuarine resources.

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BIOLOGICAL DATA ON BERRY ISLANDS (BAHAMAS) QUEEN CONCHS, *STROMBUS GIGAS*, WITH MARICULTURE AND FISHERIES MANAGEMENT IMPLICATIONS

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ABSTRACT

Biological data designed to assess the mariculture potential of queen conchs, *Strombus gigas*, and to aid in management of stocks in the Berry Islands, Bahamas, were collected from March 1980 to February 1983. Juveniles congregated in shallow areas adjacent to cays with strong currents. Growth of queen conchs differed among cays and seemed related to conch density. Average growth rates from several cays in the Berry Islands showed that growth was slower than that reported for queen conchs in other areas in the Caribbean. Estimated survival of juvenile queen conchs (about 10 cm) was 57-80% per month, or 2-9% annually. Yield per recruit from this population can be maximized by harvesting the animals at about 15 cm, which is the size at onset of lip formation but may be below the size at maturity. Presently, potential for increasing queen conch production through intensive and/or extensive mariculture seems low because of high hatchery costs, lack of dependable mass-rearing techniques, high predation on young released in nature, and slow growth of penned conchs.

The queen conch, *Strombus gigas*, a giant marine snail which is a major food resource in the Caribbean, Bahamas, and some Central American nations, has been exploited by subsistence and commercial fishermen for centuries. During the last several decades, recreational conch fisheries have developed and expanded considerably, placing high fishing pressure on these stocks. Until recently there has been little scientific research directed at improving production from existing stocks. The present study was designed to obtain biological data to fulfill this need in the Berry Islands, Bahamas.

Based on its high fecundity, feeding habits, limited migration habits, and high market demand, queen conch appears to be a desirable candidate for both intensive mariculture (enclosed) and extensive mariculture (released into nature to augment natural stocks) (Berg 1976; Brownell 1977; Brownell et al. 1976; Brownell and Stevely 1981). Success of either type of mariculture is dependent upon technical ability to mass-rear queen conch inexpensively from eggs on a dependable basis, and on knowledge of optimal natural habitats for raising juveniles to a sufficiently large size for either release in nature or for grow-out for market.

Our research on hatchery methods and potential of queen conch mariculture is described in Siddall (1983) and Iversen (1983), and the role of predators in limiting the size of conch populations is described in Jory (1982), Jory and Iversen (1983), and Iversen et al. 1986. Much of the information needed to assess feasibility of increasing queen conch production through mariculture is directly relevant to management of wild stocks. Specific objectives of the Berry Islands field work were to obtain data on age and growth, survival, and optimal habitat for rapid growth and high survival of early life stages. Based on this information, we make recommendations for management of wild stocks.

Our study area, the Berry Islands, lies on the northeastern edge of the Great Bahamas Bank (lat. 25°35′N, long 77°45′W) about 190 km east of Miami, FL (Fig. 1). This area is characterized by small cays, shallow sand flats (2-4 m deep) with abundant turtle grass, *Thalassia testudinium*, beds. The 30 plus islands are located on the west side of the N.E. Providence Channel and north of the Tongue of the Ocean. The islands are generally low-lying and covered with dense undergrowth, Australian pines, and palm trees. Tidal currents, frequently quite strong, set in and out of the openings between cays. Most cays are privately owned and sparsely populated.

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The habitat of the juvenile queen conch in our study area consisted of a large shallow plain surrounded by deep offshore waters. With a few exceptions, large adults were found in these deep areas and channels.

METHODS AND MATERIALS

Collections and observations were made at stations on adjacent cays: Little Whale Cay, Whale Cay, Vigilant Cay, Little Cockroach Cay, Bird Cay, Cat Cay, and Frazer's Hog Cay (Chub Cay) (Fig. 1). Twenty-three field trips were made to the Berry Islands from February 1980 through February 1983, each lasting 4-5 days.

The two methods used to obtain growth estimates were tagging-recapture and size-frequency analysis (Cassie 1954). After trying several different tags for conchs, we found that a thin plastic tag measuring 9.5 × 22.3 mm, obtained from the Floy[3] Tag Co. (Seattle, WA) was satisfactory. It was easily seen and suitable for even the small (ca 2-3 cm) conchs we tagged. A spot on the spire of conchs to be tagged was cleaned and dried, and the tag was affixed with underwater epoxy. We found these tags remained on wild conchs for about 2 years with indications of only a few being shed, of the 2,775 conchs we tagged and released at the sites mentioned above.

For growth estimates we measured queen conchs to the nearest mm along the anterior-posterior axis using a measuring board. Significant differences in growth rates of tagged conchs among cays and size classes were tested by analysis of variance. A Student-Neuman-Keuls test was used to detect significant differences. Differences were considered significant for all statistical tests at the $P = 0.05$ level. Mean values include 95% confidence intervals.

We derived whole animal weight-shell length relationships for queen conchs by measuring whole animal weight after removing conchs from their shells. We then removed everything but the foot to

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

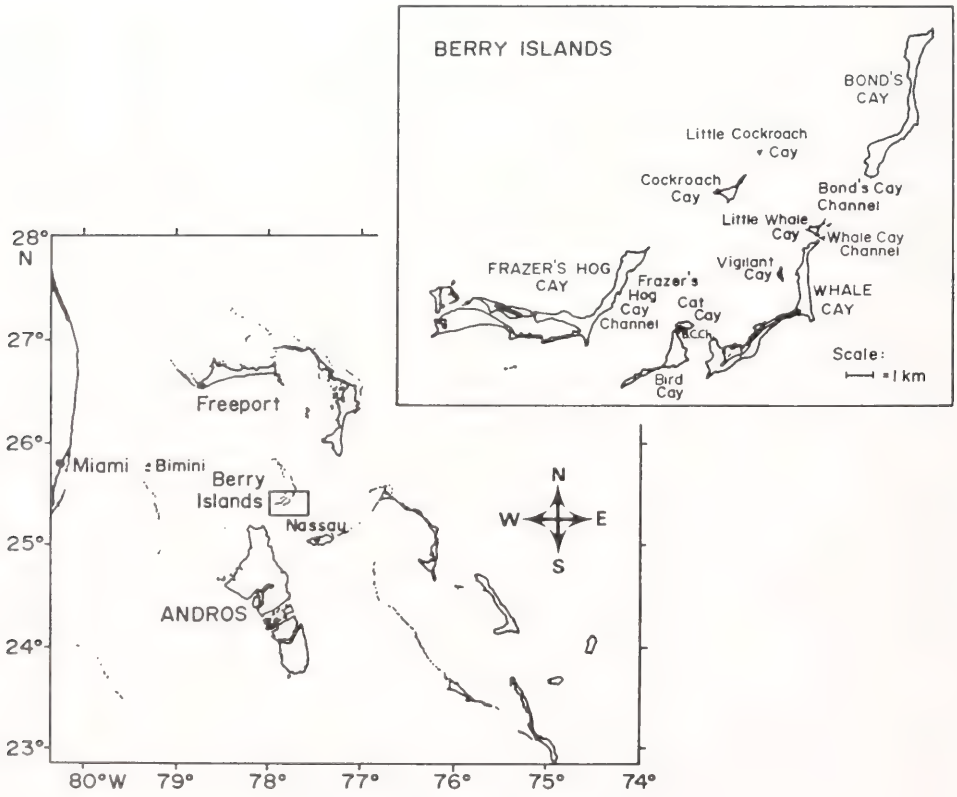


FIGURE 1.—Location of study site.

measure market weight. Significant differences in weight-length and whole animal weight-market weight relationships of conchs among cays were determined by analysis of covariance. Survival rates were obtained from the decrease in numbers of tagged queen conch at each of the tagging sites using Jackson's formula for monthly estimates and Heincke's formula for annual estimates as described in Everhart et al. (1975).

We used pens and cages of varying sizes to evaluate the feasibility of intensive mariculture. Six pens, each 25 m^2, were constructed with walls of monofilament webbing 30 cm high, held up by buoys. Pen walls were held in close contact with the bottom by heavy chains and stakes driven into the bottom, and were stocked with conchs 10-15 cm at densities of 1 or 2 conchs/m^2. Tagged conchs in this size range released in the vicinity of the pens served as controls.

Two additional large pens, 90 and 100 m^2 in area, were planted with 1 conch/m^2, the conch in the size range of 10-15 cm. Various studies on growth and survival in pens ran from 1 to 15 months.

Three wooden floating cages were used to measure growth and survival of small conchs (2-5 cm) over a 1-yr period. They were covered with fine NITEX 4 mm screening and measured 1 × 1 × 0.6 m, stocked with 50 conchs; 0.61 × 0.61 × 0.61 m, stocked with 10 conchs; and 1.6 × 1.2 × 0.6 m, stocked with 100 conchs.

Searches for small, young-of-the-year queen conch (<3 cm) were made by towing a dredge, by sieving sand samples with 4 mm mesh, by towing divers, by walking and digging on tide flats, by towing a shrimp try net (3 m opening and 1.3 cm stretched mesh), and by a suction dredge (Iversen et al. 1986).

To assess density of wild queen conch stocks in shallow water, counts were made along 100 m transects perpendicular and parallel to the shore. All queen conchs lying within 1 m of either side of the transect were counted. Significant differences in density of conchs among cays were tested by analysis of variance.

Most searches for queen conch were made during the day. To determine if this animal's burying activity varied between day and night, we conducted day-night counts at several cays and in our pens, and found no differential burying activity. Previous studies in the Virgin Islands (Randall 1964) and Puerto Rico (Appeldoorn and Ballantine 1983) reported no day-night differences in burying activity.

RESULTS AND DISCUSSION

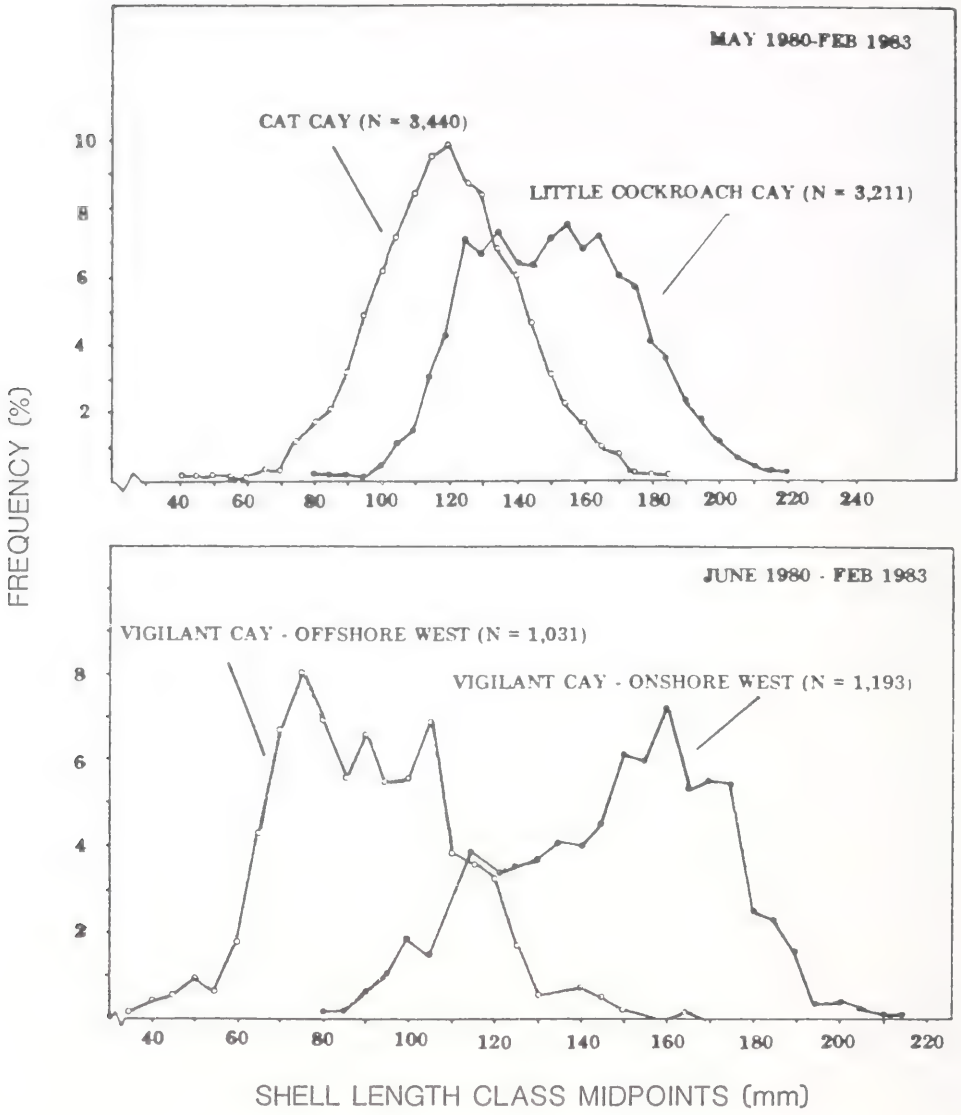
Queen Conch Distribution and Movement

Queen conchs sampled ranged from 2 to 26 cm in length (Fig. 2). The smallest conchs (<10 cm) were found on tidal flats, in shallow waters (<1 m), mostly on sandy bottoms with depressions. The largest juveniles were found in high concentrations near shores of cays, many exposed on low tides. Concentrations of adults with flared lips almost without exception were found in deep water (>3 m). Juveniles were found associated with cays having tidal flats, available food (microalgae and detritus), beaches with a gradual slope, and good water circulation. None was found in the large, open shallow-water areas between cays.

On all 23 field trips, young-of-the-year queen conchs were sought in the course of our regular field activities. The largest concentrations of young were found on the tidal flats between Bird Cay and Cat Cay (Iversen et al. 1986). Lack of shell epibionts on conchs and extensive searching suggested that small queen conchs live in the substrate and in rubble depressions until they are about 0.5 yr old, or about 3-5 cm long, at which time they are found on the tidal flats and nearshore areas in the Berry Islands. Size-frequency distributions (Table 1) showed that smallest individuals spawned the previous year (estimate based on laboratory-reared queen conchs by Siddall [1983], Brownell [1977], and others) appeared in winter, spring, and early summer.

Large juvenile queen conchs (10-18 cm) were easily located on the substrate surface all year long, generally in shallow water. Relatively few lipped queen conchs (N = 109; mean size = 19.3 ± 0.5 cm) were found during the study, most in channels 6 m deep although a few individuals were seen in shallow waters characteristic of most of our study sites. At least one lipped conch was recorded for all areas except Frazer's Hog Cay and Bird Cay-Cat Cay tidal flats. The smallest lipped conchs were found at Cat Cay ($\bar{X}$ = 14.8 ± 2.6 cm; N = 6). Lipped conchs were found every month except February, July, September, and December, with most found in April (N = 46) and October (N = 39). The distribution and seasonal occurrence of lipped conchs may reflect fishing pressure as much as potential reproductive activity.

Studies by Randall (1964), D'Asaro (1965), Brownell (1977), and Weil and Laughlin (1984) indicated that queen conchs have a protracted spawning season as long as March to October. Average length



of lipped conchs reported for the Virgin Islands was 20.4 cm (Randall 1964). Randall noted that lipped conchs sampled in the Berry Islands were smaller in length than conchs taken elsewhere in the Bahamas, or in the Virgin Islands.

Without exception, tagged queen conchs stayed at the cays where they were released, including transplanted queen conchs from nearby cays. It is possible that we did not observe migration because the majority of conchs we sampled were juveniles. Hesse (1979) reported that adult queen conch in Turks and Caicos ranged farthest (about 2 km) from the tagging site and made seasonal migrations offshore in fall and inshore in spring, while juveniles moved <1 km. Weil and Laughlin (1984) reported similar movements for adult and juvenile queen conchs in Venezuela.

Queen Conch Density by Areas

Since the density of queen conch in local areas can affect growth (Alcolado 1976; Weil and Laughlin 1984; Appeldoorn and Sanders 1984), we made density estimates at each of our sampling sites. The mean density of queen conchs at all locations studied, based on 100 m transects taken perpendicular to shore, was $\bar{X} = 7.9 \pm 1.2$ conchs/10 m^2. Highest mean densities were found at Bird Cay

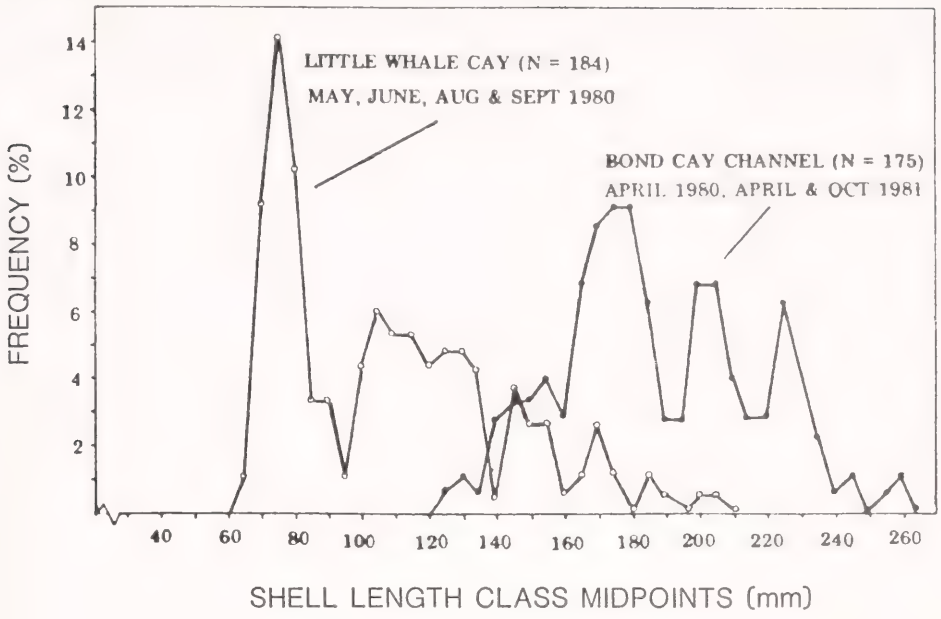


FIGURE 2.—Shell length distribution of queen conchs in the Berry Islands.

TABLE 1.—Size-frequency distribution of queen conch at Little Cockroach Cay (May 1980-April 1981).

Length (cm)	1980								1981			
	May	June	July[1]	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.[1]	Mar.	Apr.
8.0-9.0	1										2	
9.0-9.9	1											1
10.0-10.9	7	3						1	6		3	2
11.0-11.9	7	7		2				10	18		16	16
12.0-12.9	31	16		4	1			18	45		54	36
13.0-13.9	32	27		14	5	5	1	8	25		58	34
14.0-14.9	35	25		25	12	11	5	7	12		19	20
15.0-15.9	54	34		32	17	27	17	11	13		16	6
16.0-16.9	66	42		48	24	21	15	7	9		11	5
17.0-17.9	37	34		45	25	36	27	5	4		2	4
18.0-18.9	8	8		35	22	44	36	2	3		4	3
19.0-19.9	3	2		9	19	22	18	2	1		1	2
20.0-20.9				2	3	8	15	3	3		2	2
21.0-21.9				1		3	3		1		1	
Totals	282	198		217	128	177	137	74	140		189	131
Lipped conchs	0	0		1	0	1	3	0	1		0	0

[1]No data.

Channel, $\bar{X}$ = 19.6 ± 2.6 conchs/10 m^2, followed by Vigilant Cay west, $\bar{X}$ = 13.5 ± 3.1 conchs/10 m^2, and Vigilant Cay east, $\bar{X}$ = 12.2 ± 2.9 conchs/10 m^2. Lowest mean densities were found at Little Cockroach Cay, $\bar{X}$ = 1.5 ± 0.7 conchs/10 m^2 and Little Whale Cay north, $\bar{X}$ = 3.3 ± 0.7 conchs/10 m^2 (Table 2).

The mean queen conch density for all locations combined varied between June, September, and November. Density was highest in June ($\bar{X}$ = 9.9 ± 0.3 conchs/10 m^2, N = 978) followed by November ($\bar{X}$ = 6.7 ± 0.4 conchs/10 m^2, N = 673) and September ($\bar{X}$ = 6.0 ± 0.3 conchs/10 m^2; N = 722).

Queen conchs were randomly distributed over the 100 m transect at all locations except Cat Cay and Vigilant Cay, according to the results of a serial ran-

domness test (Zar 1974). Conchs were especially clumped at Cat Cay, all appearing within 10 m of shore, effectively making their densities much higher than were reported for 100 m transects (Table 2).

Queen conch densities reported for other areas in the Caribbean were generally lower, ranging from 0.8-5.2 conchs/10 m^2 in Cuba (Alcolado 1976), 0.01 conchs/10 m^2 in U.S. Virgin Islands (Wood and Olsen 1983), 0.9 conchs/10 m^2 in the Turks and Caicos (Hesse 1979) to 0.1-21 conchs/10 m^2 ($\bar{X}$ = 4.2 conchs/10 m^2) in Los Roques, Venezuela (Weil and Laughlin 1984).

TABLE 2.—Average density of queen conchs by sampling sites.

Sampling site	Average density (conchs/10 m^2 ± 95% C.I.)	N
Little Cockroach Cay	1.5 ± 0.7	88
Little Whale Cay (North)	3.3 ± 0.7	66
Vigilant Cay (West)	13.5 ± 3.1	808
Vigilant Cay (East)	12.2 ± 2.9	733
Bird Cay Channel	19.6 ± 2.6	391
Cat Cay (North)	4.2 ± 1.2	249
Cat Cay (East)	6.2 ± 3.3	372
Whale Cay	6.2 ± 1.7	123

Growth of Queen Conch by Season, Location, and Size

Seasonal Growth

Based on all data collected between February 1980 and June 1982, there was a significant ($P < 0.001$ ANOVA) seasonal difference in mean length of untagged individuals. Queen conchs measured during winter were smaller than those measured during other seasons (Table 3).

Nearly all growth of juvenile queen conchs in our study took place during the warm summer months, May-September. At Cat Cay, for example, mean growth of tagged conchs ranged from 0.44 to 1.63 cm per month during the summer, and from 0.18 to 0.30 cm per month during the remainder of the year. This is consistent with studies by Randall (1964) on queen conch in St. Croix, U.S. Virgin Islands; by Alcolado (1976) in Cuba; and by Appeldoorn (1985) on small juveniles in Puerto Rico. Our small caged conchs (2.4-3.6 cm at tagging), held for 1 year, increased 3.56 cm on the average; 92% of this increase (3.27 cm) took place between April and October.

TABLE 3.—Mean length of untagged queen conchs collected in each season between February 1980 and June 1982.

Season	Months	Mean length (cm)	N
Winter	December January February	11.9 ± [1]1.8	1,432
Spring	March April May	12.9 ± 1.1	3,475
Summer	June July August	12.6 ± 1.2	3,317
Fall	September October November	13.0 ± 1.3	2,943

[1] ± 95% confidence interval.

Growth by Location and Size

To examine the effect of location and size on growth, mean monthly growth of penned and unpenned tagged queen conch was compared within 3 size groups (<9.6 cm, 9.7-15.3 cm, >15.4 cm) by location. Densities of penned conchs (10-20 conchs/10 m^2) were higher than densities of unpenned conchs (2-20 conchs/10 m^2, $\bar{X}$ = 8) measured in the field. In every size class, unpenned conchs grew significantly faster ($P < 0.001$, ANOVA). Among unpenned conchs, there was a significant interaction effect of location and size on mean monthly growth. Large conchs (>15.4 cm) at Little Cockroach Cay, where density was lowest, grew faster than all other sizes. Small conchs (<9.6 cm) grew the next fastest, followed by intermediate-sized conchs (Table 4). Queen conchs at Cat Cay and Vigilant Cay offshore west, where densities were higher, grew slower as

TABLE 4.—Comparison of mean monthly growth rates (cm) for unpenned queen conchs. Underlined locations indicate significant difference in monthly growth between locations as determined by Student-Newman-Keuls test.

Size class	Tagging locations		
9.6 cm	Vigilant Cay Offshore West	Little Whale Cay	Cat Cay
	(0.40) ± [1]0.3 N = 198	(0.48) ± 0.03 N = 13	(0.50) ± 0.04 N = 114
9.6-15.3 cm	Cat Cay	Little Whale Cay	Little Cockroach Cay
	(0.25) ± 0.02 N = 385	(0.40) ± 0.03 N = 186	(0.48) ± 0.02 N = 248
15.3 cm		Little Whale Cay	Little Cockroach Cay
		(0.31) ± 0.07 N = 23	(0.50) ± 0.03 N = 146

[1] 95% confidence interval.

a group than queen conchs at Little Whale Cay and Little Cockroach Cay (Table 4). Alcolado (1976) also reported that queen conchs in Cuba grew slower in areas of high density (5.2 conchs/10 m^2) than in areas of low density (0.08 conchs/10 m^2). Appeldoorn and Sanders (1984) reported similar results in a laboratory experiment on small juvenile conchs.

There was no significant interaction effect between size and location on growth of penned queen conchs. Smallest conchs in cages grew fastest, followed by intermediate-sized conchs (Table 5). There were insufficient data for large penned conchs to estimate their mean monthly growth. Among the intermediate-sized conchs where density was known, mean monthly growth was highest in pens with the lowest density (0.1/10 m^2 compared with 0.2/10 m^2).

Randall's (1964) penned queen conchs (mean length 6.2 and 7.5 cm, range 5.2-8.0 cm; N = 25) grew slowly (0.26 cm/month), but these measurements were made during winter months. Pen size was not specified. In another experiment, Randall placed 16 tagged conchs (19.0-20.0 cm, $\bar{X}$ = 19.4 cm) in a "60 ft by 140 ft elliptical fenced area" during winter and reported average growth of 0.1 cm/month through April when the experiment was discontinued.

Growth rates for our larger penned conchs (mean length 10.3 cm) approximated Randall's rates (0.1 and 0.2 cm/month), even though our data were recorded throughout the year. Growth rates were higher for our smaller conchs (mean length = 4.6 cm; mean growth = 0.4 and 0.2 cm/month) than for larger conchs.

Length at Age

Estimates of length at ages 1-3 were obtained for Berry Islands queen conchs by length-frequency analysis (Cassie 1954) and by fitting the von Bertalanffy equation to tagging data. Distinct length modes of 634 queen conchs measured in October 1980 were present at 7.6, 12.5, and 17.0 cm, suggesting length at ages 1, 2, and 3, respectively.

Parameters in the von Bertalanffy (1938) equation were estimated by fitting a Walford (1946) line to tagging data from Cat Cay, Vigilant Cay, Little Whale Cay, and Little Cockroach Cay (N = 117). Fitting a Walford growth line requires that the growth rate decreases with age. Since the largest queen conchs at Little Cockroach Cay grew faster than the middle-sized juveniles, we excluded these data from our calculations and obtained the following estimates of average length by ages (Table 6).

Age	*Lt (cm)*	
I	8.3	
II	12.2	
III	15.4	
IV	18.1	With L_∞ = 30.0
		K = 0.20
		t_0 = −0.65.

Our estimates of length at age from both length-frequency analyses and von Bertalanffy estimates of tagging data (excluding Little Cockroach Cay data) indicate that queen conch in the Berry Islands grow more slowly than those in the Virgin Islands and some of the areas in Cuba where density was low (0.8 conchs/10 m^2). We suggest that the higher densities of queen conch and cooler water temperatures in the Berry Islands may slow their growth relative to other areas.

Length-Weight Relationship

Whole animal weight(minus the shell)-shell length relationships were derived for queen conch sampled at Chub Cay (N = 39), Frazer's Hog Cay (N = 32), and Bird-Cat Cay Channel (N = 34). Log_{10}

TABLE 5.—Comparison of mean monthly growth rates (cm) for penned queen conch. Underlined locations indicate no significant difference in monthly growth between locations as determined by Student-Newman-Keuls test.

Size class	Tagging location						
9.6 cm	Pen 7		Pen 9	Small Wood Cage		Large Wood Cage	
	(0.04) ± [1]0.07 N = 25		(0.21) ± 0.06 N = 25	(0.24) ± 0.06 N = 38		(0.35) ± 0.06 N = 66	
9.7-15.3 cm	Pen 5	Pen 6	Pen 7	Pen 2	Pen 9	Pen 3	Pen 1
	(−0.05) ± 0.04 N = 38	(−0.01) ± 0.01 N = 38	(0.04) ± 0.02 N = 64	(0.08) ± 0.02 N = 48	(0.11) ± 0.04 N = 56	(0.15) ± 0.03 N = 45	(0.17) ± 0.05 N = 34
15.4 cm	Insufficient data						

[1]95% confidence interval.

TABLE 6.—Estimates of queen conch length (cm) at age from the Caribbean.

Year class	Berry Islands,[1] Bahamas a	Berry Islands,[1] Bahamas b	Puerto Rico[2]	U.S. Virgin Islands St. John[3]	U.S. Virgin Islands St. Thomas[4]	Cuba[5]	Venezuela[6]
I	7.3	8.3	8.8	10.8	9.0	7.9-11.2	7.6
II	12.5	12.2	12.6	17.0	12.6	12.50-18.8	12.8
III	17.0	15.4	18.0	20.5	15.7	15.5-24.3	18.0
IV		18.1				17.4-28.3	
L (cm)		30.3		26.0		20.8-38.3	
K		0.20		0.52		0.287-0.571	
t_0		−0.65		0		−0.12-0.13	
N	634	103	193	104	301	63-284	161

[1]This study - size frequence (a) and von Bertalanffy fit to tagging data (b).
[2]Berg 1976 - size frequency.
[3]Berg 1976 and Brownell et al. 1976 - von Bertalanffy fit to Randall's (1964) tagging data.
[4]Wood and Olsen 1983 - size frequency.
[5]Alcolado 1976 - von Bertalanffy fit to tagging data from 7 locations.
[6]Brownell 1977 - size frequency.

(weight)-Log_{10} (length) relationships best fit the data. Analysis of covariance showed that queen conch at Frazer's Hog Cay and Chub Cay had similar whole animal weight-shell length relationships but that both differed from conchs at Bird-Cat Cay Channel. Therefore, two relationships were developed.

Frazer's Hog-Chub Cay

$$\text{Log}_{10}(\text{whole animal weight}) = -2.40 + 3.57 \times \text{Log}_{10}(\text{shell length})$$

$$r = 0.95 \qquad N = 71$$

Bird-Cat Cay Channel

$$\text{Log}_{10}(\text{whole animal weight}) = -1.36 + 2.84 \times \text{Log}_{10}(\text{shell length})$$

$$r = 0.93 \qquad N = 34.$$

Mean lengths of queen conch at Frazer's Hog Cay ($\bar{X} = 15.6 \pm 0.7$ cm) and Chub Cay ($\bar{X} = 18.6 \pm 0.8$ cm) were significantly ($P < 0.001$) larger than those at Bird-Cat Cay Channel ($\bar{X} = 13.6 \pm 0.1$ cm). Shell length-whole animal weight relationships changed with size. Smaller conchs ($\bar{X} = 13.6 \pm 0.1$ cm) increased in weight per unit length faster than did larger conchs ($\bar{X} = 17.0 \pm 0.7$ cm).

We found a close linear relationship between whole animal weight and meat weight of Berry Islands queen conch which did not vary among areas:

$$\text{market weight} = 0.65\,(\text{whole animal weight}) + 6.00$$

$$N = 105;\ r = 0.97.$$

The relationship between shell length and animal weight, although significant ($P < 0.001$) was not as close:

$$\text{market weight} = 11.47\,(\text{shell length}) - 50.69$$

$$N = 105;\ r = 0.84.$$

Table 7 gives the numbers of different aged queen conchs in the Berry Islands needed for 1 pound of market meat. Using the whole animal weight-shell length and whole animal weight-market weight relationships developed above and assuming size at lip formation (14.8-19.3 cm) is the size at harvest, 4-10 queen conchs are needed to produce 1 pound of meat (Table 7). In the Berry Islands 6-8 conchs are needed to make 1 pound of market meat, as opposed to 2-3 and 3-4 conchs/pound from other areas in the Bahamas (Berg 1981). The high numbers of queen conchs per pound of market meat from the Berry Islands may be partially explained by their stunted growth.

TABLE 7.—Number of Berry Island queen conch required to make 1 pound of market meat.[1]

Age	von Bertalanffy estimated length at age	Whole animal weight/conch (g)	Market wt (lb)	No. of conchs to make 1 lb of meat
I	8.3	[2]17.8	0.04	26
II	12.2	[2]53.1	0.09	11
III	15.4	[3]73.0	0.12	9
IV	18.1	[3]130	0.20	5
IV[4]	19.3	164	0.25	4

[1]Market meat = (0.65) (whole animal weight − shell weight) + 6.
[2]Shell length (cm) converted to whole animal weight (gm) with Bird-Cat Cay Channel regression $\log_{10}$ (weight) = −1.36 + 2.84 $\log_{10}$ (shell length).
[3]Shell length (cm) converted to whole animal weight (g) with Frazer's Cay-Chub Cay regression $\log_{10}$ (weight) = −2.40 + 3.57 $\log_{10}$ (shell length).
[4]Mean size of lipped queen conchs sampled in Berry Islands.

Survival-Mortality

Estimates of monthly and annual survival of unpenned and penned queen conchs in the Berry Islands were derived from tagging studies. The estimates assume that tags are not overlooked, that tags do not fall off or affect survival, that the tagged population is similar to the untagged population in all other respects and that no emigration occurs during the experiments.

Monthly survival rate of unpenned queen conchs ranged from 57 to 80%, depending on location (Table 8). The estimates for Little Cockroach, Vigilant, and Cat Cays are the most reliable, because more conchs were tagged over a longer period of time at these three locations than at others. Annual survival was low for these areas, ranging from 2 to 9%. These proportions result in estimates of total instantaneous mortality rate, Z, from 2.41 to 3.91, considerably higher than those reported by Alcolado (1976) for queen conch in Cuba (annual survival 15-35%, Z from 1.06 to 1.90) or by Wood and Olsen (1983) for recruited queen conch in St. Thomas, U.S. Virgin Islands (Z from 0.22 to 1.80).

Appeldoorn (1985) found mortality of small juvenile queen conchs (<6.4 cm) in Puerto Rico higher at $Z = 8.62$, or an annual survival of 0.02%. In a recent study of large juveniles and adults, Appeldoorn (in press) estimated annual $Z = 2.67$, with M plus emigration = 1.53 and $F = 1.14$. Our survival estimates are probably low because of problems inherent to tagging studies mentioned above.

Survival of penned queen conchs in 4 of our pens was much higher than survival of unpenned animals (Table 8). Monthly survival ranged from 90 to 97% for penned animals, and annual survival ranged from 28 to 73%. However, all conchs died in the 2 deeper water pens. We attribute much of the increased survival rate of queen conch in our best pens to reduced predation, although an undetermined portion of the increase is due to eliminating emigration and the increased probability of finding tagged animals in an enclosure. However, the positive influence of increased survival must be balanced with the slow growth rates of all but the smaller (4.5-8 cm) sizes in pens.

Seasonality of burying, as demonstrated in our penned conch data and by Hesse (1979), using unpenned queen conch, can affect the estimated survival rate because some of the animals cannot be found. Based on our results in pens, the possible error in survival estimate due to burying would probably be relatively small because over about a 1-yr period, a total of 25 out of 200 queen conchs (about 12%) were buried; however, on any single monitoring trip only 1 or 2 individuals were buried.

Causes of Mortality

It is well documented that predation plays a significant role in the survival of queen conchs (Jory 1982; Jory and Iversen 1983; Iversen et al. 1986) and will not be detailed here. After settlement, at all sizes, even flared lipped, thick-shelled adults are subject to predation by large turtles and fishes; however, the rate of predation is significantly higher on the small, thin-shelled juveniles (2-5 cm) and decreases as the animals grow.

Based on our observations, those of our colleagues and reports in the literature, predation, rather than abiotic factors of the environment, or parasites and disease, seem to be the most important causes of queen conch mortality. Hence, stock size after settlement appears to be predator-controlled. This is not an unusual finding when the wide range of species of queen conch predators feeding on all sizes of conch is considered (Randall 1964; Jory and Iversen 1983; Iversen et al. 1986), together with the important role that predation plays in the mortality of many other mollusks (Jory et al. 1984).

TABLE 8.—Survival estimates for Berry Islands queen conchs.

	Unpenned conchs				Little Whale Cay penned conchs					
	Little Cockroach Cay	Vigilant Cay	Cat Cay	Little Whale Cay	Small wooden cage	Large wooden cage	Pen 1	Pen 2	Pen 3[1]	Pen 4
Monthly survival[2]	0.80	0.72	0.80	0.57	0.96	—	0.93	0.97	0.92	0.90
Annual survival[3]	0.02	0.09	0.09	0.02	0.69	0.13	0.36	0.73	0.36	0.28
Number tagged _ conch released	282	169	418	59	26	15	25	30	50	25
$\bar{X}$ size (cm)	15.0	8.4	11.4	13.0	7.2	7.6	10.5	10.2	10.2	10.5
Range (cm)	8.2-22.3	6.5-11.7	8.1-19.1	8.6-20.6	5.0-8.0	4.5-9.0	8.5-12.0	6.0-12.5	6.0-12.0	8.5-12.5

[1]Only 11 months involved.
[2]Monthly survival estimates made using Jackson's formula.
[3]Annual survival estimates made using Heincke's formula.

Management Implications: Yield per Recruit

Yield-per-recruit analysis, based on our estimate of the von Bertalanffy growth equation and total mortality from tagging, was conducted for the shallow-water queen conch populations in the southern Berry Islands. Yield per recruit was computed from the model given by Beverton and Holt (1957) which assumes that growth rate, susceptibility to capture, and natural mortality remain constant after age of recruitment.

We believe that the combined data from unpenned queen conch in all areas (excluding Little Cockroach Cay) gave us accurate estimates of growth and mortality. We estimated maximum meat weight for Berry Island conchs to be 463 g, based on the shell length to whole animal weight regression from the Frazer's Hog Cay-Chub Cay area, which was the largest sample. Age at recruitment was assumed to be 3 years (corresponding to a length of 15.4 cm). Maximum age of queen conch, based on L_∞ = 30.3 cm and our von Bertalanffy equation, was 11 years.

Using an overall mean annual survival of 7%, Z is 2.66. Estimates of yield per recruit were obtained for a range of values of M between 0.50 and 2.6. F varied between 0.16 and 2.66, by increments of 0.50, and t_0 varied between 1 and 5 years by increments of 1.10 for each level of M. This analysis probably encompassed any value of M and F that actually existed during the study.

At M = 0.50, age liable to capture that maximizes yield in weight per recruit is 3 years, over a range of F from 0.16 to 2.66. Thus, if fishermen take queen conch of approximately 15 cm and larger, they would maximize the yield available from the population. At all values of M above 0.50, results indicate a stage of underfishing because yield in weight per recruit increases over the range of F and decreases with increasing age liable to capture.

The results of yield-per-recruit analyses are limited for several reasons. First, larger, faster growing queen conchs from Little Cockroach Cay were excluded from the analyses; the von Bertalanffy equation did not describe well the growth of conchs from the full data set. Second, the range of sizes in the tagging studies did not accurately reflect the range of sizes in the total queen conch population in the southern Berry Islands. Most data were collected on immature conchs (before lip formation) that were living on shallow flats near islands. While the purpose of analyzing prospects for mariculture were adequately fulfilled by these data, they should not be used for fisheries management because they, for the most part, do not include the larger adults found in deeper channels between cays.

While these data are preliminary, they indicate an important management principle that was also determined for queen conch in the U.S. Virgin Islands by Wood and Olsen (1983); namely, that maximum yield per recruit is obtained at age of first harvest, which is just at onset of lip formation. In the Virgin Islands they found the maximum yield could be obtained by harvest between 3 and 5 years, at an average length of 15.78-19.1 cm. Maximum yield per recruit may occur below onset of maturity, however, since there is some evidence that queen conch may not be reproductively active until some time after lip formation (Wilkins et al., in press).

Mariculture Potential

Queen conch mariculture potential, one objective of this study, was investigated as a possible means to increase conch production in the Bahamas. A hatchery was established at the University of Miami. Techniques were developed for mass-rearing queen conch from egg masses collected in the wild through the larval stages (Siddall 1983). However, because of the high hatchery costs and high mortality associated with planting young mollusks in the wild (Iversen et al 1986; Jory et al. 1986), supplementing natural conch stocks by extensive mariculture does not appear to be economically feasible at this time. We placed juvenile conchs in pens at densities slightly higher than those in nature and found very slow growth, meanwhile experiencing considerable difficulty in physically maintaining the pens. Further, complete mortalities occurred in some pens, which we cannot explain.

Our results suggest that, for the numbers of queen conch required for supplementing natural stocks, the techniques available could probably only be successful in certain well-protected areas. In Bonaire, a degree of success has been reported by Hensen (1983). For intensive mariculture, unless a special area is found with good water exchange, natural food availability, where most predators can be excluded, and large juvenile conchs released, this technique of attempting to enhance production does not appear to have much potential at this time. With additional research, particularly on developing dependable hatchery techniques and cost-efficient means of predator protection, intensive mariculture may some day play a useful role in increasing production.

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REVISION OF THE GAMBA PRAWN GENUS *PSEUDARISTEUS*, WITH DESCRIPTION OF TWO NEW SPECIES (CRUSTACEA: DECAPODA: PENAEOIDEA)

ISABEL PÉREZ FARFANTE[1]

ABSTRACT

The genus *Pseudaristeus* (family Aristeidae) is widespread in the Indo-West Pacific where five species—*P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., and *P. sibogae*—have been found at depths between 719 and 1,785 m; another species, *P. speciosus*, occurs in the southwestern Atlantic, where it was taken at 4,847 m. Females of *Pseudaristeus* possess a styliform, long rostrum, 0.70-1.40 as long as the carapace; most males have shorter ones 0.20-0.57, but some have been found in which the rostrum is as long as that of the females. This suggests that in this genus, as in *Aristeus*, at certain stages of the life cycle, males develop a long rostrum. Following a revised definition of the genus, a key to the species, a synonymy, the location of the types, type-locality, and a list of specimens examined are given for each species. Detailed morphological accounts, including intraspecific variation, accompany statements of maximum sizes, and geographic and bathymetric ranges. The description of *P. gracilis* is the first to take into consideration adult material. In discussing relationships, *P. crassipes*, *P. kathleenae*, and *P. protensus*, sympatric off the coast of India, are shown to constitute a rather homogenous group somewhat distantly related to the other very distinctive members of the genus.

The deep-sea "gamba prawns" of the genus *Pseudaristeus* are widely distributed at depths of 719-1,785 m in the Indo-West Pacific—from the Gulf of Aden and off Natal, South Africa to the Philippines—where five (*P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., *P. sibogae*) of the six species recognized herein are found. The sixth (*P. speciosus*) occurs in the southwestern Atlantic, off northeastern Argentina. It is unlikely that members of the genus occur in the northwestern Atlantic, including the Gulf of Mexico and the Caribbean, where, although intensive collecting have been conducted, no *Pseudaristeus* have been taken.

The large gamba prawns (reaching as much as 47.5 mm carapace length, about 150 mm total length) that occur at shallower depths might, in the not too distant future, make a minor, but highly esteemed, contribution to the commercial catches of penaeoids in certain areas of the Indo-West Pacific, as do members of other deep-sea genera (*Aristaeomorpha*, *Aristeus*, and *Plesiopenaeus*) of the family Aristeidae.

The genus *Pseudaristeus* has been poorly understood largely because the original descriptions of the first three recognized species, *P. speciosus*, *P. gracilis*, and *P. crassipes*, are inadequate for separating them, and the illustrations of the latter two, although well rendered, are of little help. Incomplete descriptions and inadequate illustrations were primarily responsible for subsequent assignment of specimens of two new species described here to *P. crassipes*, which, like them, occurs in the waters off India.

Availability of the rich collections of *Pseudaristeus* made by the U.S. Bureau of Fisheries steamer *Albatross* during the Philippine Expedition, 1907-10, and the loan of critical material from several museums have enabled me to make detailed studies of all six species of the genus. Included in the accounts of each are numerous diagnostic characters which have not been previously recognized in the four described species. One of these characters is the sinuous ventral antennular flagellum found in male *P. gracilis*, which not only allows a ready identification of these animals but constitutes another significant element for the interpretation or a better understanding of the relations of the members of *Pseudaristeus* to those of the closely allied *Aristeus*.

PRESENTATION OF DATA

In the account of the species, most of the terminology used follows that proposed and illustrated by Pérez Farfante (1969, 1977). The anterolateral carina, a unique feature of one member of *Pseudaristeus*, which has not been cited by me previously,

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extends between the gastro-orbital and branchiostegal-hepatic carinae. The names of various parts of the eye, adopted from Young (1956, 1959), were recently employed and illustrated by Pérez Farfante (1985). The measurement of rostrum length (RL) is the linear distance from apex to orbital margin, that of carapace length (CL) is the distance between orbital margin and the midposterior margin of the carapace, and, finally, that of total length (TL) is the distance from the apex of the rostrum to posterior end of the telson. All measurements are made to the nearest 0.5 mm. The petasmata have been described and all but one depicted unfolded; the illustrations were made from stained specimens. Because more than one species have been found in lots reported by various authors under a single name and new species are described herewith from waters from which records have been previously cited, the map is based on only the specimens examined by me. Scales accompanying the illustrations are in millimeters.

Abbreviations of the repositories of the specimens examined during this study are as follows:

BMNH - British Museum (Natural History), London.
MP - Muséum National d'Histoire Naturelle, Paris.
USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C.
ZMA - Zoologisch Museum, Amsterdam.
ZMB - Zoologisches Museum der Humboldt - Universitat, Berlin.
ZSI - Zoological Survey of India, Calcutta.

GENUS *PSEUDARISTEUS* CROSNIER, 1978

Hemipenaeus Bate 1881:186 [part].
Aristaeus Wood-Mason and Alcock 1891:278 [part].
Aristeus Anderson 1896:91.
Pseudaristeus Crosnier 1978:81 [type species, by original designation, *Aristaeus crassipes* Wood-Mason 1891:281. Gender masculine].

Diagnosis.—Body slender, covered with densely set minute setae. Rostrum long in females and short or long in males; armed with 2 dorsal teeth; epigastric tooth distinctly posterior to first rostral, situated about 0.1 CL from orbital margin. Antennal and branchiostegal spines present; orbital, pterygostomian, and hepatic spines lacking. Cervical sulcus crossing postrostral carina (rarely only reaching it); postcervical sulcus extending to postrostral carina; gastro-orbital, antennal, branchiostegal-hepatic, and branchiocardiac carinae strong; hepatic sulcus long, usually fusing with branchiocardiac sulcus and descending obliquely almost to margin of branchiostegite. Abdomen with dorsomedian carina extending from fourth through sixth somites; elongate sixth somite bearing pair of long cicatrices. Telson produced posteriorly in sharp, median spine and with posterior 0.4 of length armed with 4 pairs of small, movable, lateral spines. Eye with well-developed cornea and dorsoventrally depressed peduncle bearing mesial tubercle; basal article not produced in scale. Antennular peduncle length about 0.55 CL; prosartema rudimentary, consisting of short stump bearing brush of long setae; dorsal flagellum short, about 0.4 length of antennular peduncle, and flattened; ventral flagellum long, no less than 2.75 CL, and filiform. Mandibular palp (Fig. 1*A*) reaching to about base of ischiocerite (third article of antennal peduncle), distal article suboval and much smaller than basal. Palp of first maxilla unsegmented (Fig. 1*B*). Second maxilla and first and second maxillipeds as illustrated (Fig. 1*C-E*). Exopods on all maxillipeds but lacking on pereopods. Petasma with dorsomedian lobule short, only about 0.4 length of petasma; ventromedian lobule with rib narrow proximally, broadening to level of distal end of dorsomedian lobule where reaching mesial margin, and continuing almost to end of lobule; ventral costa distally free, not attached to dorsolateral lobule; endopod of second pleopod bearing appendices masculina and interna. Thelycum of "open type", with large, lanceolate median plate on sternite XIII. Well-developed podobranchia on second and third maxillipeds and first and second pereopods, those on pereopods subequal in size. One arthrobranchia on somite VII and two on VIII through XIII, all well developed except very small anterior one on somite VIII. Pleurobranchia on somites IX through XIV, that on XIV well developed, remaining ones much smaller. Nonbifurcate, large epipod on somites VII through XII, that on XII subequal in size to that on XI. (Modified from Crosnier 1978.)

It seems worth emphasizing that although the rostrum is long in females, 0.70-1.40 CL, and relatively short in most of the males examined, 0.20-0.57 CL, I have found one male in each of two species with long rostra, 0.70 and 1.40 CL.

Five species known from the Indo-West Pacific are *P. crassipes*, *P. gracilis*, *P. kathleenae* n. sp., *P. protensus* n. sp., and *P. sibogae*; and the one from the southwestern Atlantic is *P. speciosus*. The species from the Indo-West Pacific have been taken at depths between 750 and 1,785 m and that from the southwestern Atlantic at 4,847 m. These depths and all others cited are those noted for the stations

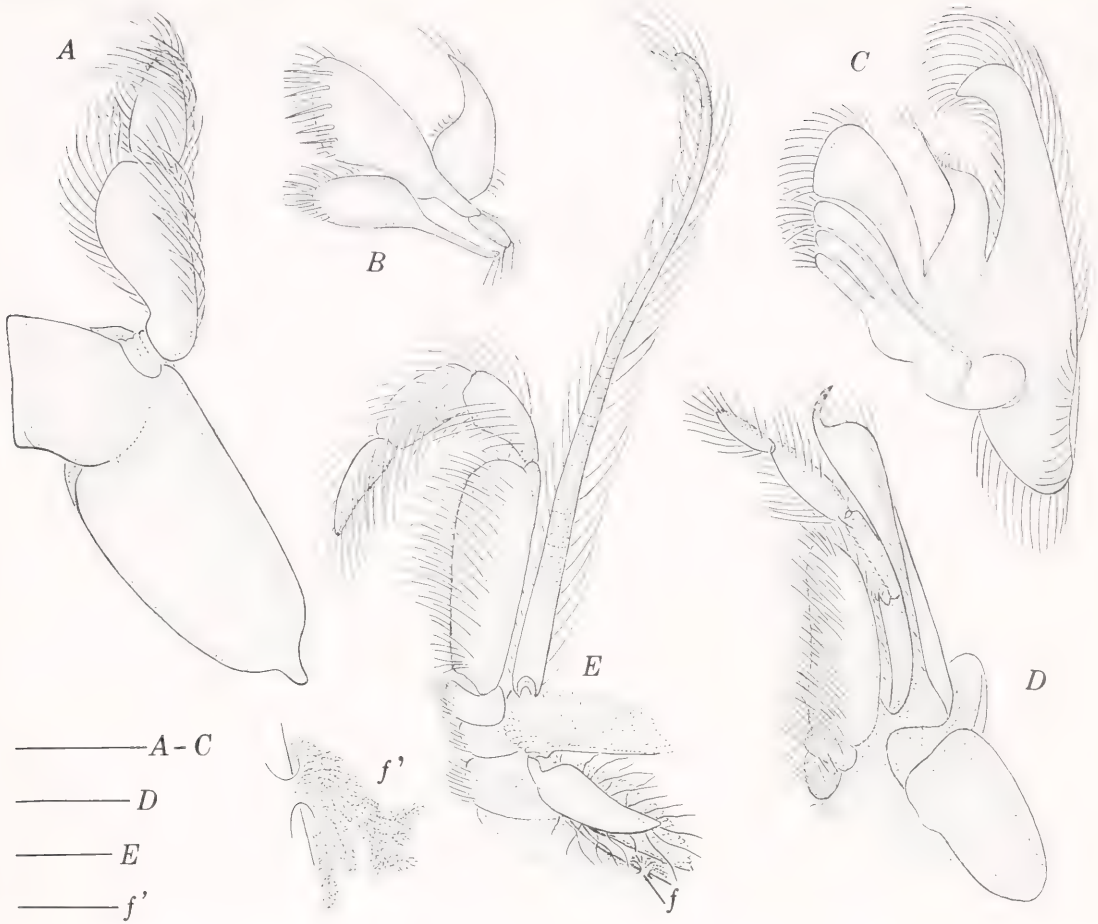

FIGURE 1.—*Pseudaristeus kathleenae* n. sp., ♀ 35 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. *A*, Mandible. *B*, First maxilla. *C*, Second maxilla. *D*, First maxilliped. *E*, Second maxilliped. *f*, Rudimentary arthrobranchia. *f'*, Enlargement of *f*. (All from left side). Scales: *A-E* = 3 mm; *f'* = 1 mm.

at which the specimens were obtained, but because open nets were used in collecting, it is not possible to ascertain the actual level at which the shrimp entered the net.

Pseudaristeus is quite close to *Aristeus*, having the same branchial formula, but differing from it in exhibiting a well-marked cervical sulcus which reaches the dorsomedian carina of the carapace and in possessing a postcervical sulcus. Among the members of *Pseudaristeus* only males of *P. gracilis* exhibit a sinuous ventral antennular flagellum, a feature characteristic of the males of all species of the genus *Aristeus*. This similarity, together with a branchial formula common to the two genera, indicates a close affinity between members of the genera *Pseudaristeus* and *Aristeus* and is a convincing basis for the postulate that they have had a more recent common ancestor than either share with *Hemipenaeus*. The species now assigned to *Pseudaristeus* were placed in the genus *Hemipenaeus* by almost all authors in this century until Crosnier (1978) proposed that they be removed to his new genus.

Key to species of *Pseudaristeus*

1. Ventral extremity of cervical carina blunt, not forming sharp-edged arc. Anterolateral carina present. Posterior part of hepatic sulcus not fusing with branchiocardiac sulcus but extending longitudinally subparallel to latter. ..... *P. speciosus*

   Ventral extremity of cervical carina forming

sharp-edged arc. Anterolateral carina absent. Posterior part of hepatic sulcus fusing with branchiocardiac sulcus and continuing posteroventrally oblique to latter. 2

2. Optic calathus long, mesial margin at least 1.5 width of distal extremity. Pereopods covered with minute setae. . . . . *P. sibogae*

Optic calathus short or relatively so, mesial margin 1.3 or less width of distal extremity. Pereopods not covered with setae. 3

3. Thelycum with median plate of sternite XIII very long (length more than 4 times basal width), almost reaching spine on sternite XII, and narrow, maximum width 0.40 length. [Males unknown]. . . . . *P. protensus*

Thelycum with median plate of sternite XIII relatively short (length less than 3.5 times basal width) and broad or relatively broad, maximum width more than 0.40 length. . . . 4

4. Third article of antennular peduncle expanded laterally, forming strong, subtriangular projection in males and variably developed rounded prominence in females. Petasma with ventral costa neither strongly inclined distomesially nor contracted preapically. Thelycum with median plate of sternite XIII moderately broad (maximum width 0.65-0.75 length) and lacking posterolateral prominences. . . . . *P. kathleenae*

Third article of antennular peduncle not expanded laterally, forming neither strong prominence in males nor rounded prominence in females. Petasma with ventral costa strongly inclined distomesially or contracted preapically. Thelycum with median plate of sternite XIII either relatively narrow (maximum width 0.45-0.55 length) or, if broad (0.80-0.93), bearing posterolateral prominances. 5

5. Males with ventral antennular flagellum sinuous proximally and bearing narrow band of densely set small setae distal to dorsal flagellum; petasma with ventral costa markedly contracted preapically. Females with median plate of sternite XIII expanded in pair of conspicuous posterolateral prominences. . . . . *P. gracilis*

Males with ventral antennular flagellum straight proximally and lacking band of small setae; petasma with ventral costa not markedly contracted preapically. Females with median plate of sternite XIII lacking posterolateral prominences. . . . . *P. crassipes*

Pseudaristeus kathleenae, new species

Figures 1-3, 4*C*, 5-9

Aristaeus crassipes. Alcock 1901a:50 [part].

Hemipenaeus crassipes. De Man 1911:24. Kemp and Seymour Sewell 1912:17 [part], pl. 1, fig. 8. De Man 1913, pl. 2, fig. 4*a-c* and in legend to fig. 5 [under Remarks for *H. sibogae*]. Balss 1925:229 [part].

Materials.

Holotype: ♂, USNM 216710, 23.5 mm CL, 6.5 mm RL, about 88 mm TL; type-locality: Teluk Bone, Sulawesi (Celebes), Indonesia; 3°19′40″S, 120°36′30″E; 900 m; gray mud; 19 December 1909; *Albatross* stn 5657.

Paratypes: India—1 ♀, USNM 216711, collected with holotype. 1♂, ZSI 7806/10, W of Cape Comorin, Tamil Nādu, India; 7°46′N, 76°37′E; 1,225 m; 26 April 1911; *Investigator* stn 388. 2 ♂, ZSI, S of Cape Comorin, Tamil Nādu, India; 7°36′N, 78°05′E; 556-595 m; 10 April 1900; *Investigator* stn 268.

Indonesia—1 ♀, ZMB, off W Sumatra; 0°39′S, 98°52′E; 750 m; 31 January 1899; *Valdivia* stn 191. 1 ♂, ZMA, eastern Flores Sea; 7°24′00″S, 118°15′12″E; 794 m; fine gray mud, with some radiolariae and diatomes; 6 April 1899; *Siboga* stn 45. 1 ♀, USNM, Teluk Bone, Sulawesi (Celebes); 3°17′40″S, 120°36′45″E; 885 m; gray mud; 19 December 1909; *Albatross* stn 5656. 3 ♀, USNM, Teluk Bone, Sulawesi (Celebes); 3°32′40″S, 120°31′30″E; 933 m; gray mud; 19 December 1909; *Albatross* stn 5658. 1 ♀, USNM, W of Halmahera; 0°35′00″N, 127°14′40″N, 127°14′40″E; 795 m; fine gray sand, mud; 27 November 1909; *Albatross* stn 5619.

Philippines—2 ♀, USNM, Cagayan Is, Sulu Sea; 9°38′30″N, 121°11′00″E; 929 m; gray mud, coral sand; 31 March 1909; *Albatross* stn 5423. 1 ♂ 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°32′30″N, 123°58′06″E; 1,033 m; gray mud; 10 June 1909; *Albatross* stn 5460. 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°40′57″N, 123°57′45″E; (549 m); sand; 16 June 1909; *Albatross*

stn 5463. 1 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°39′42″N, 123°40′39″E; 914 m; gray mud; 17 June 1909; *Albatross* stn 5465. 1 ♀, USNM, Verde Island Passage, N of Mindoro; 13°36′11″N, 120°45′26″E; 622 m; fine sand; 20 January 1908; *Albatross* stn 5114. 4 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°35′27″N, 123°37′18″E; 878 m; gray mud; 18 June 1909; *Albatross* stn 5467. 2 ♂ 5 ♀, USNM, Lagonoy Gulf, E of southern Luzon; 13°36′48″N, 123°38′24″E; 914 m; green mud; 18 June 1909; *Albatross* stn 5469.

Diagnosis.—Optic calathus relatively short, mesial margin 1.0-1.3 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle expanded laterally, forming large subtriangular projection in males, but weak to rounded prominence in females; males with ventral antennular flagellum never sinuous, and ultimate article of third maxilliped strongly curved, spatulate and bearing patch of strong, rigid setae. Pereopods not covered with minute setae. Petasma with ventral costa only slightly inclined distomesially, and ventral surface of dorsolateral lobule lacking setae. Thelycum with plate of sternite XIV rather long and produced at either side in short anterolateral hood; median plate of sternite XIII moderately long (not nearly reaching spine on sternite XII), rather broad (maximum width 0.65-0.75 length) but not expanded posterolaterally in conspicuous prominences.

Description.—Body slender (Fig. 2), densely studded with minute setae. Rostrum in males usually short, its length 0.25-0.45 CL (but in one male, 24 mm CL, 1.4 CL), and roughly lanceolate; in females long (Fig. 3), 1-1.15 CL (but in one female 23 mm CL, 0.70 CL), relatively deep and convex basally, styliform and slightly unturned anteriorly. Rostral plus epigastric teeth 3; rostral teeth situated variably in males, basally in females. Adrostral carina strong, in males almost reaching apex, in females (and in male with long rostrum) extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine as long as or longer than antennal and acutely pointed. Cervical sulcus crossing postrostral carina (rarely only reaching it) at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt except for sharp strongly arched ventral extremity; weak postcervical sulcus reaching, but not crossing, postrostral carina at about 0.70 CL from orbital margin. Postrostral carina, extending 0.75-0.80 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina well defined; antennal carina rather short; branchiostegal-hepatic carina long, raised and sharp. Orbitoantennal sulcus shallow; hepatic sulcus fusing with branchiocardiac sulcus, then turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by carina, long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by weak groove, latter approaching cervical sulcus anteriorly and ending about level of postcervical sulcus posteriorly.

Eye (Fig. 4*C*) with optic calathus relatively short, length of mesial margin 1.0-1.3 times distal width; mesial tubercle strong and situated between distal 0.25 and 0.30 length of margin.

Gnathal appendages, except third maxilliped, illustrated in Figure 1.

Antennular peduncle with stylocerite produced in sharp spine falling conspicuously short of mesial base of distolateral spine; latter small and sharp; third article in adult males uniquely produced in large subtriangular or ax-head shaped projection (Fig. 2) directed ventrolaterally, in females (Fig. 5*B*) expanded laterally in broadly rounded prominence. Dorsal flagellum reaching between distal 0.20 and 0.15 of scaphocerite; ventral flagellum straight and long, although incomplete in all specimens examined, in one male with 19 mm CL its length at least 2.75 times CL.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum at least 1.25 times TL of shrimp.

Third maxilliped sexually dimorphic. In males (Fig. 5*A*) with penultimate article often slightly to strongly inflated proximally, compressed and produced in strong, subelliptical or acuminate process (overhanging proximal part of ultimate article) distally; article also bearing brush of long thickly set setae on both mesial and lateral surfaces, and dense row of setae along distal margin of process. Ultimate article subspatulate, strongly arched, not expanded basally, bearing distally dense patch of strong, rigid setae on lateral surface, proximalmost setae short and more distal ones considerably longer; terminal margin with tuft of very long flex-

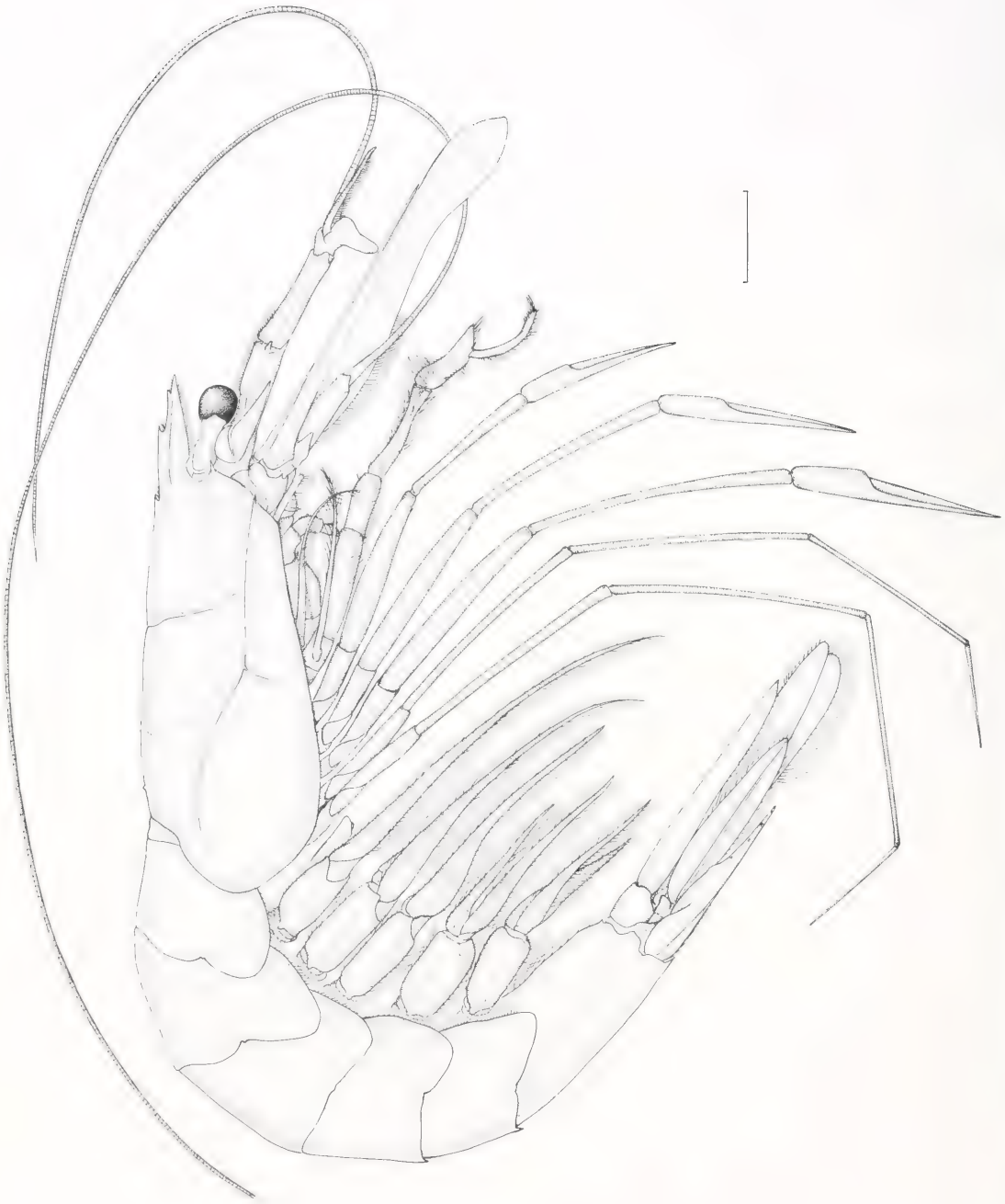

FIGURE 2.—*Pseudaristeus kathleenae*, holotype ♂ 23.5 mm CL, Teluk Bone, Sulawesi (Celebes), Indonesia. Lateral view. Scale = 6 mm.

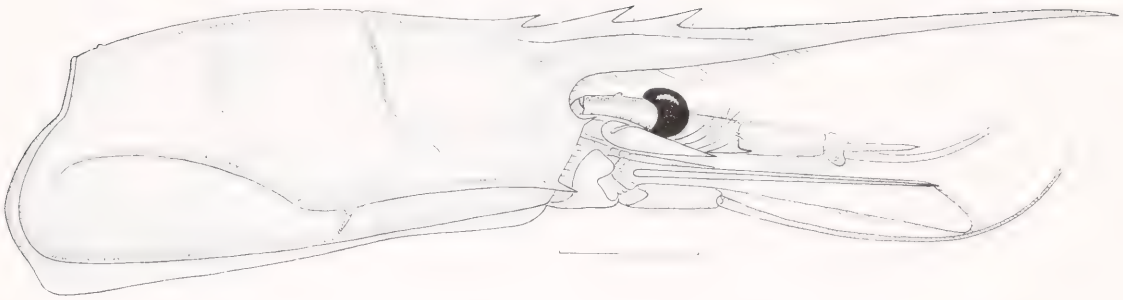

FIGURE 3.—*Pseudaristeus kathleenae*, ♀ 37 mm CL, Verde Island Passage, north of Mindoro, Philippines. Anterior region, lateral view. Scale = 10 mm.

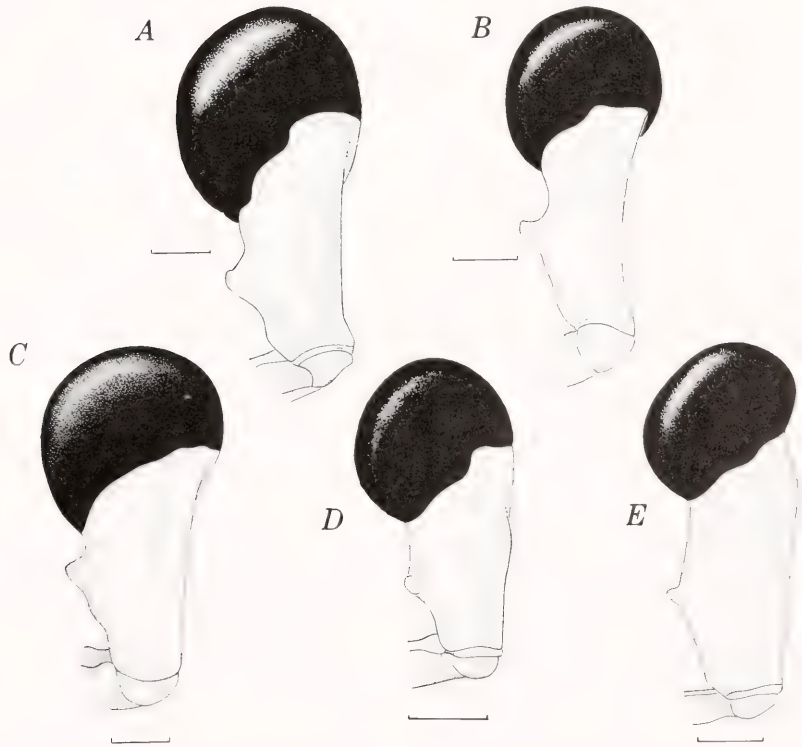

FIGURE 4.—Eyes. *A*, *Pseudaristeus crassipes*, ♂ 28.5 mm CL, south of Cape Comorin, Tamil Nādu, India. *B*, *P. gracilis*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines. *C*, *P. kathleenae*, holotype ♂ 23.5 mm CL, Teluk Bone, Sulawesi, Indonesia. *D*, *P. protensus*, holotype ♀ 40 mm CL, west of Evēral Gujārat, India. *E*, *P. sibogae*, ♀ 47.5 mm CL, south of Pulau Muna, Sulawesi, Indonesia. Scales: *A*, *B*, *C* = 1 mm; *D*, *E* = 2 mm.

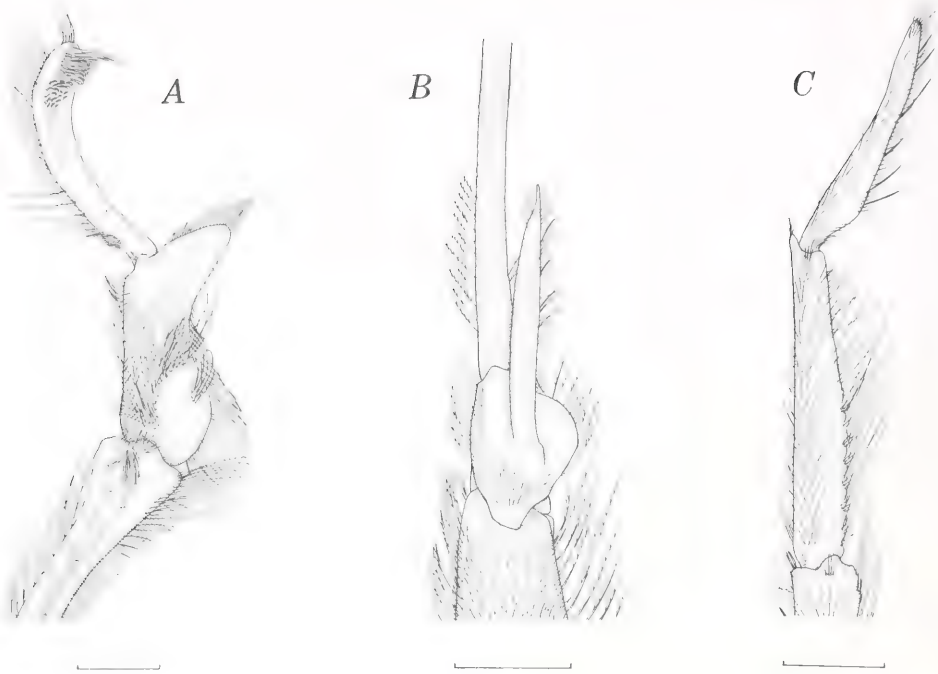

FIGURE 5.—*Pseudaristeus kathleenae*: *A*, ♂ 26 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines, distal articles of left third maxilliped, lateral view. *B*, ♀ 39 mm CL, Teluk Bone, Sulawesi, Indonesia, distal articles of right antennular peduncle and flagella, dorsal view. *C*, same ♀, distal articles of left third maxilliped, dorsal view. Scales = 2 mm.

ible setae, and entire ventral margin supporting numerous ones. In females (Fig. 5*C*), ultimate article slender, flattened, broadening slightly from narrow base, then tapering gently to blunt apex.

Pereopods not covered with setae; first and second with broad, compressed merus bearing small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending from posterior 0.75 of fourth somite posteriorly through sixth somite and produced in spine on caudal margin of last 3 somites; sixth also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus weak, usually distinct along anterior 0.75 length of telson, and flanked by paired longitudinal dorsolateral ridges; bearing 4 pairs of movable spines: 3 at about 0.60, 0.75, 0.85 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its own length.

Petasma (Figs. 6, 7*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule extending distally as far as dorsolateral lobule and bearing elongate, lapel-like flap

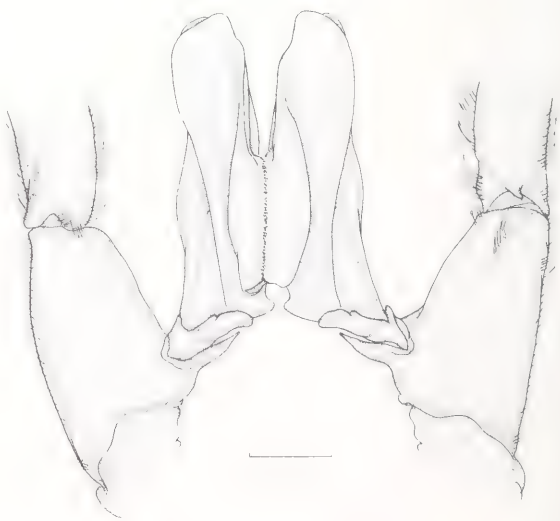

FIGURE 6.—*Pseudaristeus kathleenae*, ♂ 24.5 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. Petasma and proximal part of first pleopods, dorsal view. Scale = 2 mm.

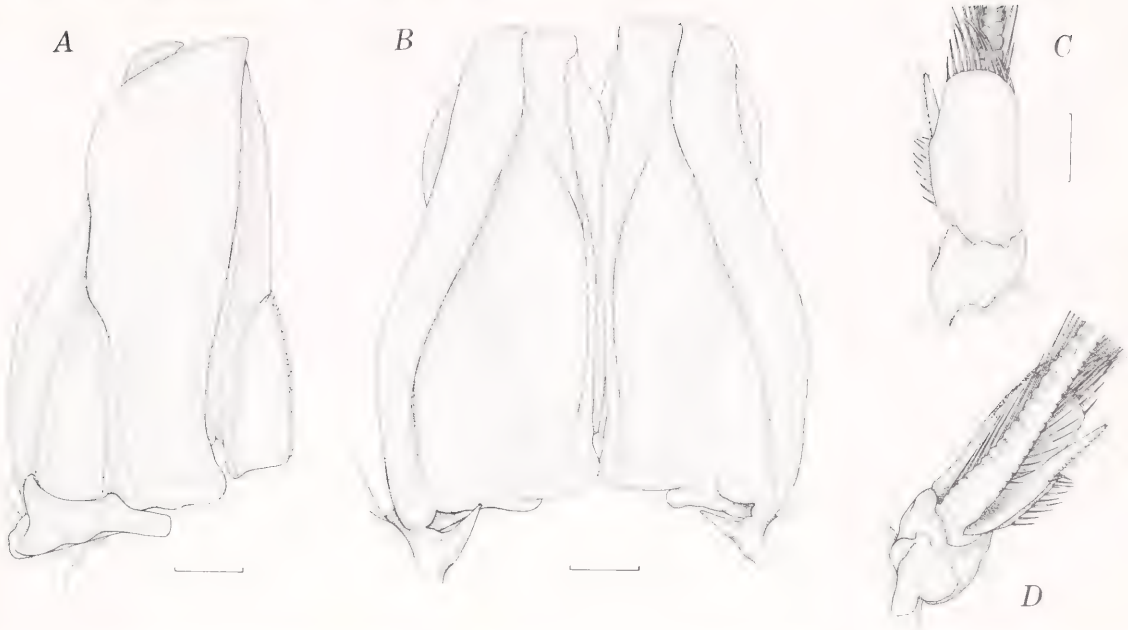

FIGURE 7.—*Pseudaristeus kathleenae*, holotype ♂, 23.5 mm CL, Teluk Bone, Sulawesi, Indonesia. *A*, Petasma, dorsolateral view of left half. *B*, Ventral view. *C*, Right appendices masculina and interna, and basal sclerite of endopod, dorsal view. *D*, Ventral view. Scales = 1 mm.

distoventrally along mesial margin. Dorsolateral lobule sclerotized, expanding distolaterally before tapering to subangulate mesial apex, its distolateral margin strongly curved; ventral surface, exhibiting arched slender rib, lacking setae. Ventral costa gently sinuous, only slightly inclined distomesially, its terminal part forming truncate blade lying free but against ventral surface of dorsolateral lobule.

Appendix masculina (Fig. 7*C*, *D*) roughly obovate, with proximal part curving ventrally embracing appendix interna; its distal margin bearing long setae and mesial margin bearing short, more numerous ones. Appendix interna roughly triangular and subequal in length to appendix masculina.

In males, sternite XIV with setose anteromedian tubercle; plate of sternite XIII elongate (length 2-3 times basal width), broadly rounded anteriorly and produced in minute apical spine bearing tuft of long setae.

Thelycum (Fig. 8) with setose, moderately long plate of sternite XIV either traversed by shallow groove posteriorly or broadly depressed, and with anteromedian margin varying from distinctly concave to slightly convex, plate produced at either side in short anterolateral hood; fossa immediately anterior to plate very conspicuous and bearing pair of small oblique ridges. Median plate of sternite XIII,

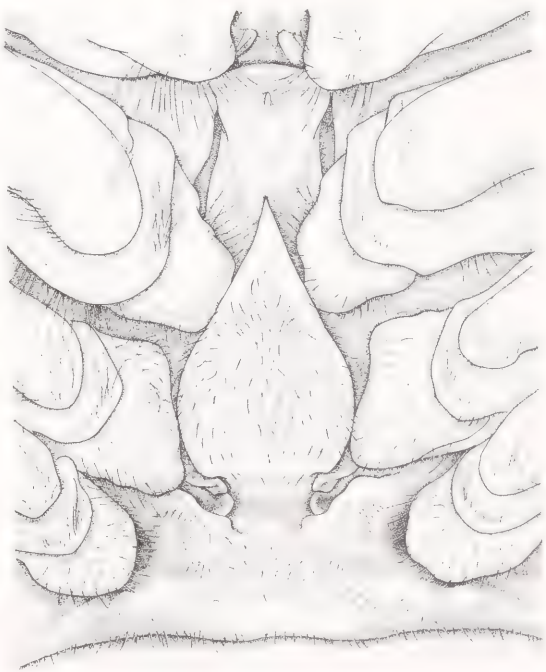

FIGURE 8.—*Pseudaristeus kathleenae*, ♀ 47 mm CL, Lagonoy Gulf, east of southern Luzon, Philippines. Thelycum. Scale = 2 mm.

also covered with setae, moderately long (length 3-3.5 times basal width), falling considerably short of spine on sternite XII, broadly lanceolate (maximum width 0.65-0.75 length), and flat or slightly excavate; posterolateral margins of plate, sometimes turned ventrally, abutting slender ridges extending posteromesially before curving laterally on margin of sternite XIII. Sternite XII minutely setose, bearing median keel ending anteriorly in anteroventrally directed sharp spine.

Maximum lengths.—Males, 24 mm CL; females, 46.5 mm CL.

Geographic and bathymetric ranges.—From west of Cape Comorin, India, through Indonesia, and northward to east of Luzon, Philippines (Fig. 9). It has been obtained at depths between 549 and 1,225 m.

Discussion.—This species differs from *P. crassipes*, with which it has been confused previously, in the following unique characteristics. In males, the third article of the antennular peduncle is strikingly produced in a subtriangular or roughly ax-head shaped lateral projection, and in females it is expanded laterally in a broadly rounded prominence. This is a feature by which the females of *P. kathleenae* can be infallibly distinguished from those of *P. crassipes* which, otherwise, are quite similar. In *P. crassipes*, the third article of the antennular peduncle of both sexes is uniform in width proximally and gradually tapers distomesially. In males of *P. kathleenae*, the penultimate article of the third maxilliped is compressed distally and produced in a strong subelliptical or acuminate process which overhangs the ultimate article; the latter is subspatulate, conspicuously curved throughout, almost uniform in width, and bears long rigid setae on the lateral surface. In the males of *P. crassipes* the penultimate article of the third maxilliped is subtriangular in cross section throughout and does not project distally in a conspicuous process but instead is rounded distally; the ultimate article is twisted, expanded basally, and weakly to conspicuously so distally, and bears lateral rows of spinules on its ventral surface.

Pseudaristeus kathleenae differs further from *P. crassipes* in features of the petasma. In the former, the dorsolateral lobule is expanded distolaterally before tapering to a subangulate mesial apex; also the ventral costa is sinuous and does not turn strongly distomesially from its basal part. In contrast, the dorsolateral lobule is not expanded distolaterally in *P. crassipes*, tapers to broadly elliptical apex, and the ventral costa is almost straight basally before turning rather abruptly distomesially. Finally, in females of *P. kathleenae* the median plate of sternite XIII is broader than that in *P. crassipes*, its maximum width ranging from 0.67 to 0.75 rather than from 0.45 to 0.55 as it does in the latter.

In females of *Pseudaristeus* the rostrum is long, almost as long or considerably longer than the carapace, whereas, in males it is usually short, less than 0.33 the length of the carapace. Among the 8 males of *P. kathleenae* examined in this study, one possesses a rostrum that is 1.4 times the length of the carapace (longer than that of any female examined), and among the three available males of *P. crassipes*, the rostrum of one, although proportionally not so long, is 0.7 as long as the carapace. Perhaps these males with long rostra are not as rare as one might anticipate. This suggestion is based on a study by Burukovsky and Romensky (1972) in which they noted considerable variation in the length of the rostrum in another aristeid, *Aristeus varidens*, occurring in the eastern Atlantic from Ghana to Angola. It was well known that in all genera of Aristeidae the rostrum of females is much longer than that of males; however, they found that although the majority of males of this gamba prawn have a relatively short rostrum, in almost 30% of them it is long. Also, they noted that in both sexes the rostrum decreases proportionately with increasing size (a fact well established for penaeoid species) and that this age-dependent variation is different for the sexes: in small females the rostrum may exceed 1.5 times the length of the carapace, whereas in large ones it is about as long as the carapace; in small males the length of the rostrum may be almost 1.5 times that of the carapace, but as they grow it decreases to 0.1-0.5 times. Nevertheless, in individuals of the same size they found that the range of variation is smaller in females than in males. Their study demonstrates that sexual dimorphism in the length of the rostrum, thought to be typical of aristeids, disappears at least in small males of *A. varidens*. This too might obtain in members of *Pseudaristeus*, but because of the lack or paucity of males of all 6 species I am unable to conduct a meaningful investigation of variations in RL/CL. Because no correlation was observed between variations in the length of the rostrum and changes in the petasma or in the structure of the gonads in males with short and long rostrum which would indicate sexual change, Burukovsky and Romensky suggested that the reduction of the rostrum, more marked in males than in females, might be associated with the transition from a benthic to a bathypelagic existence undergone by members of the family Aristeidae.

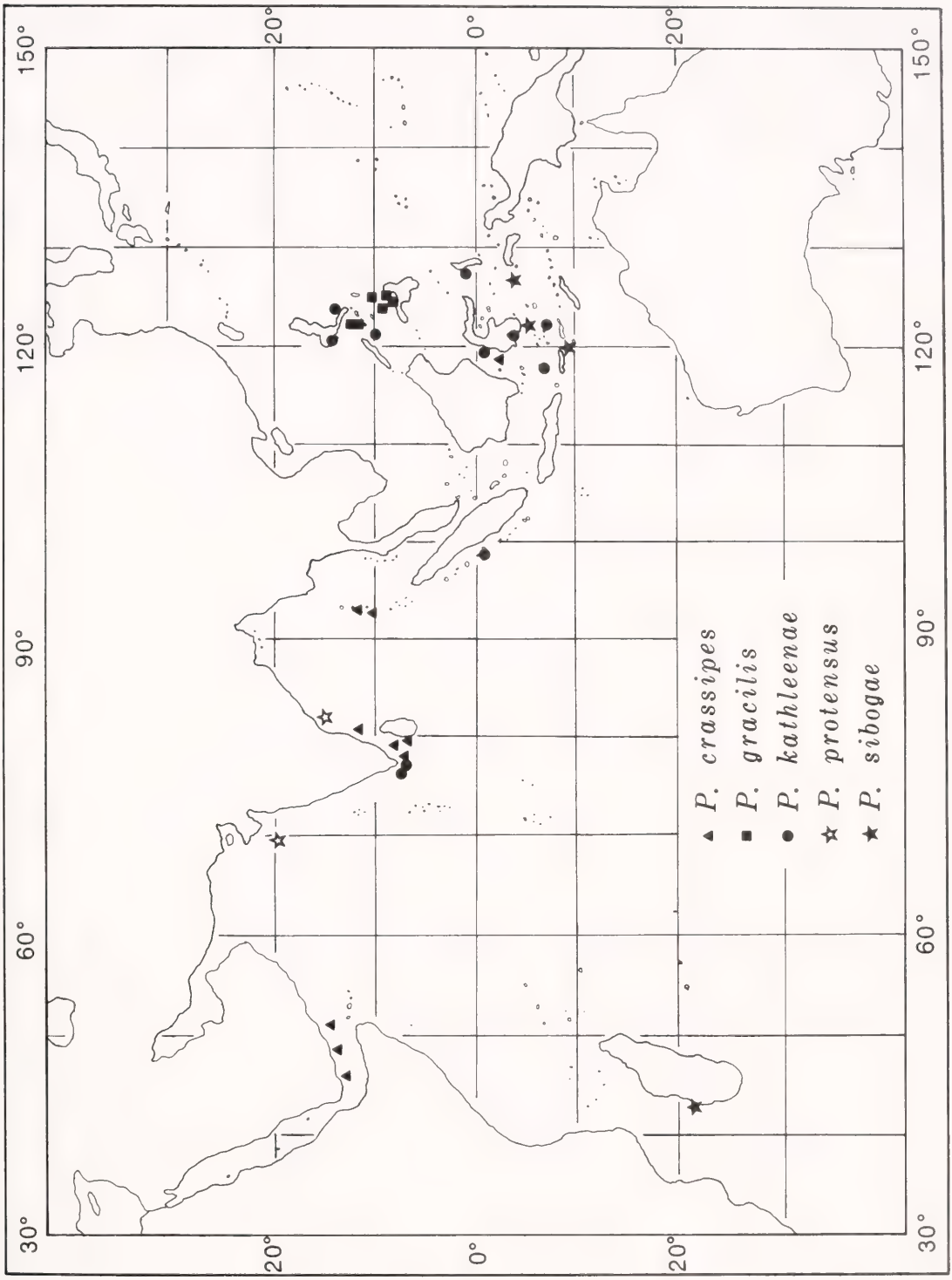

FIGURE 9.—Ranges of *Pseudaristeus crassipes*, *P. gracilis*, *P. kathleenae*, *P. protensus*, and *P. sibogae*.

Only a few of the available specimens of this species still have entire pereopods, and even fewer have retained all 5 pereopods; in almost all, the fourth and fifth are missing, or only two or three podomeres are represented. The data obtained by me, however, seem to confirm those presented by De Man (1911) and Crosnier (1978), which indicate that the pereopods of *P. kathleenae* are more slender than those of *P. sibogae*. Their data were based on a female 31 mm CL collected by the Siboga Expedition and identified by them as "*crassipes*". This specimen was examined during the present study and is assigned herein to *P. kathleenae*.

Etymology.—I take pleasure in naming this shrimp for my daughter Kathleen P. Canet.

Pseudaristeus crassipes (Wood-Mason 1891)

Figures 4*A*, 9-13

Aristaeus crassipes Wood-Mason 1891:281, fig. 7 [syntypes: 1 ♀, ZSI 6713/9, Andaman Sea; 11°25′05″N, 92°47′06″E; 405 fm (741 m); green mud; 9 December 1890; *Investigator* stn 116. 1 ♀, ZSI 3171/9 (could not be located in ZSI, 24 November 1984, Maya Deb of ZSI, pers. commun.[2]); off SW Sri Lanka; 6°29′00″N, 79°34′00″E; 597 fm (1,092 m)]. Alcock and Anderson 1894: 147. Faxon 1895:198. Anderson 1896:91. Alcock 1901a:50 [part]; 1902:268, figs. 63, 64a, b.

[?]*Aristaeus crassipes*. Alcock 1898:74. Alcock and Anderson 1899:3. Doflein 1906:259.

Aristaeus (*Hemipeneus*) *crassipes*. Alcock 1901b:33.

Aristeus (*Hemipeneus*) *crassipes*. Alcock and McArdle 1901, pl. 49, figs. 1, 2.

Aristeus crassipes. Lloyd 1907:2.

Hemipeneus crassipes. Kemp and Sewell 1912:17 [part], pl. 1, fig. 9.

Hemipenaeus crassipes. Balss 1925:224 [part]. Ramadan 1938:49. Anderson and Lindner 1945: 301. Ramadan 1952:15, fig. 18. Sewell 1955:203. Burukovsky 1974:48. Silas and Muthu 1979:78. Not *Hemipenaeus crassipes* Monod 1974:118, figs. 7-11 [= *Aristeus virilis* (Bate 1881) and *Aristeus mabahissae* Ramadan 1938; fide Crosnier 1978:85].

Pseudaristeus crassipes. Crosnier 1978:83, fig. 30*d*; 1986:862.

Pseudaristeus sp. Crosnier 1984:22.

[2]Mayo Deb, Zoologist, Zoological Survey of India, Calcutta, India, pers. commun. 24 November 1984.

Material.

Gulf of Aden—3 ♀, BMNH + 1 ♀, USNM, off Djibouti; 13°06′12″N-13°03′00″N, 46°24′30″E-46°21′42″E; 1,061 m; 7 May 1934; green mud; John Murray Exped. stn 193. 1 ♀, ZMB, off Yemen (Aden); 13°02′N, 46°41′W; 1,469 m; 4 April 1899; *Valdivia* stn 271. 1 ♀, BMNH, off Yemen (Aden); 13°41′N-13°40′N, 48°17′E-48°19′E; 1,295 m; 15 October 1933; John Murray Exped. stn 33. 1 ♀, BMNH, off Yemen (Aden); 14°36′06″N-14°38′42″N, 51°00′18″E-50°57′42″E; 1,269 m; 4 May 1934, John Murray Exped. stn 184.

India—1 ♀, ZMB, Arabian Sea, *Investigator* [stn not given]. 2 ♂, ZSI, S of Cape Comorin, Tamil Nādu; 7°36′N, 78°15′E, 1,017-1,088 m; green mud, sand; 10 April 1900; *Investigator* stn 268. 1 ♀, MP, Gulf of Mannar; 8°11′N, 79°03′E; 1,035 m; 28 July 1981; *Safari II* stn 4, CP 06. 1 ♂, ZSI, off Chidambaran, Tamil Nādu; 11°29′45″N, 80°02′30″E; 816 m; 19 March 1901; *Investigator* stn 280. 1 ♂ 1 ♀, BMNH, S of Andaman Is, 10°06′N, 92°29′E; 1,289 m; *Investigator* stn 315.

Sri Lanka—2 ♀, ZSI, NW of Colombo; 6°54′30″N, 79°34′30″E; 878 m; green mud; 20 October 1898, *Investigator* stn 250.

Indonesia—1 ♀, MP, Strait of Makassar; 2°04′24″S, 118°46′54″E; 1,710-1,730 m; 9 November 1980; *Corindon II* stn 286.

Diagnosis.—Optic calathus relatively short, mesial margin 0.9-1.1 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum not sinuous and ultimate article of third maxilliped twisted, markedly dilated proximally, less so distally, and bearing ventrolateral rows of minute spines. Pereopods not covered with minute setae. Petasma with distal two-thirds of ventral costa turned rather abruptly distomesially and ventral surface of dorsolateral lobule lacking setae. Thelycum with plate of sternite XIV long and produced in short anterolateral hoods; median plate of sternite XIII moderately long (not nearly reaching spine on sternite XII), rather narrow (maximum width 0.45-0.55 length), and not expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males (complete only in two) relatively short, its length 0.2 and 0.7 CL, and tapering gradually to sharp apex; in females longer,

1.15-1.25 CL, moderately deep and convex basally, styliform and slightly upturned anteriorly, but occasionally with apical extremity curving downward. Rostral plus epigastric teeth 3; rostral teeth, situated variably in males, basally in females. Adrostral carina strong, in males with short rostrum almost reaching apex, in females and in male with long rostrum extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostal carina (rarely only reaching it) at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt, except for sharp, strongly arched ventral extremity; postcervical sulcus reaching, but not crossing, postrostral carina at about 0.7 CL from orbital margin. Postrostral carina, extending 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by strong carina, deep and long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by shallow groove, latter extending anterodorsally almost to cervical sulcus and continuous posteriorly with postcervical sulcus.

Eye (Fig. 4*A*) with optic calathus relatively short, length of mesial margin 0.9-1.1 times distal width; mesial tubercle strong and situated between 0.30 and 0.45 length of mesial margin from cornea.

Antennular peduncle with stylocerite produced in sharply pointed spine falling distinctly short of, to almost reaching, mesial base of distolateral spine; latter slender and sharp. Third article never produced laterally (Fig. 10*C*); dorsal flagellum reach-

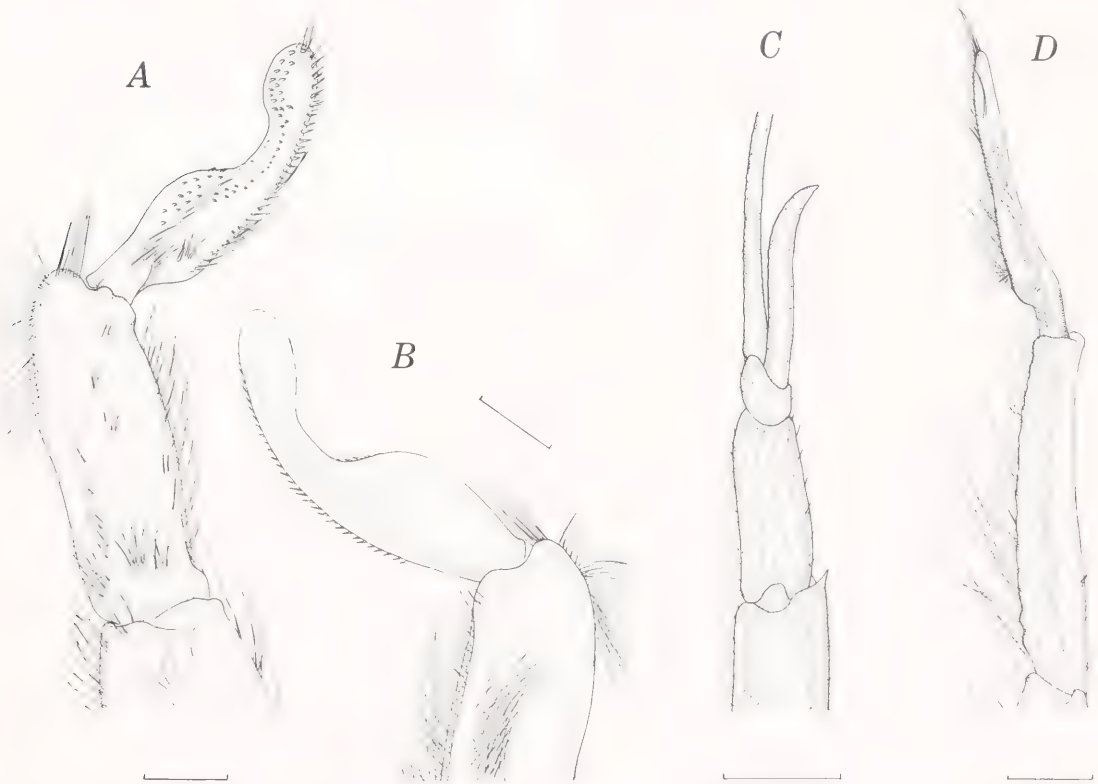

FIGURE 10.—*Pseudaristeus crassipes* (Wood-Mason): *A*, ♂ 26.5 mm CL, south of Cape Comorin, India, distal articles of right third maxilliped, ventral view. *B*, Same ♂ distal articles of right third maxilliped, dorsal view. *C*, Lectotype ♀, Andaman Sea, India, distal articles of right antennular peduncle and flagella, dorsal view (prepared from camera lucida drawings by H. C. Ghosh). *D*, ♀ 25 mm CL, south of Andaman Islands, India, distal articles of left third maxilliped, ventral view. Scales: *A*, *B*, *D* = 1 mm, *C* = 4 mm.

ing between base of distal 0.25 and end of scaphocerite; ventral flagellum straight and long, although broken in all specimens studied, in male with 22 mm CL its length 2.1 times CL.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete in all specimens examined.

Third maxilliped sexually dimorphic: Males (Fig. 10*A*, *B*) with penultimate article subtriangular in cross section, its distomesial margin not produced in conspicuous process but bluntly rounded; ultimate article twisted, expanding from short, narrow base, then narrowing and becoming concave laterally before again expanding (sometimes almost imperceptibly) distally; ventral surface with proximal, transverse comb of long setae continuous with lateral rows of minute spines extending to and around distal extremity. Females with ultimate article (Fig. 10*D*), slender, but broadening slightly mesially from short, narrow base, then tapering to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad depressed merus bearing small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending along posterior 0.75 of fourth somite through sixth, and produced in spine on posterior margin of last 3 somites; sixth somite also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus shallow, usually distinct only along anterior 0.25 length of telson, and flanked by pair of longitudinal dorsolateral ridges; bearing 4 pairs of movable spines: 3 situated at about 0.60, 0.75, 0.85 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its length.

Petasma (Fig. 11*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule extending distally almost as far as dorsolateral lobule and bearing elongate, lapel-like flap distoventrally along mesial margin. Dorsolateral lobule sclerotized, not expanded distolaterally, with lateral margin only slightly curved and distalmost part broadly rounded forming subelliptical mesial apex; ventral surface lacking setae, exhibiting conspicuous, slender, arched rib. Ventral costa almost straight basally along 0.4 of its length, then turning somewhat abruptly distomesially, its rather broad terminal part truncate (sometimes with disto-

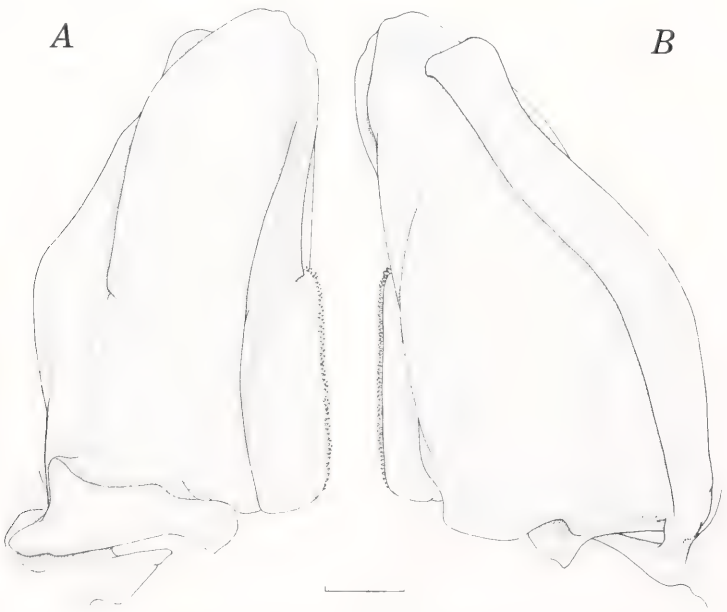

FIGURE 11.—*Pseudaristeus crassipes*, ♂ 26.5 mm CL, south of Cape Comorin, India. *A*, Petasma, dorsal view of left half. *B*, Ventral view (specimen slightly distended). Scale = 1 mm.

mesial angle slightly produced) lying free but against ventral surface of distolateral lobule.

Appendices masculina and interna like those of *P. kathleenae*. In males, plate of sternite XIII flat, ovate but produced in minute apical spine, its length 1.8-1.9 basal width; sternite XIV bearing anteromedian tubercle or low, anteriorly produced prominence.

Thelycum (Fig. 12*A*, *B*) with setose plate of sternite XIV long, transversely depressed (occasionally with median elevation), anteriomedian margin straight or slightly convex, plate produced at either side in short anterolateral hood; fossa immediately anterior to plate short and bearing pair of small, oblique, ridges. Median plate of sternite XIII, also covered with setae, moderately long (length 2.9-3.5 basal width) but falling distinctly short of spine on sternite XII, rather narrow (maximum width 0.45-0.55 length), lanceolate, tapering anteriorly from near base, occasionally from near midlength, and strongly produced in sharp apical spine; posterolateral margins of plate, usually turned ventrally, flanked by, or interlocking with, slender ridges curving laterally on margin of sternite XIII. Sternite XII minutely setose, strongly raised and crested by median carina ending anteriorly in minute spine.

Color in life crimson (Wood-Mason 1891).

Maximum lengths.—Males, 29 mm CL; females 37 mm CL.

Geographic and bathymetric ranges.—From the Gulf of Aden to the Strait of Makassar, Indonesia (Fig. 9). It has been found at depths between 741 and 1,710-1,730 m.

Variation.—This species exhibits marked variation in shape of the last 2 articles of the third maxilliped in armature of sternite XIV of males, and also in the shape of the thelycal plate of sternite XIII in females. Those articles range from moderate to very narrow widths and both the proximal and distal parts of the ultimate article may be imperceptibly to conspicuously dilated. Sternite XIV may bear either an anteromedian tubercle or a low, anteriorly produced prominence. In the few males examined, the presence of a very slender ultimate article of the third maxilliped seems to be correlated with the presence of a prominence, instead of a tubercle, on sternite XIV. Furthermore, in females the thelycal plate of sternite XIII, although always lanceolate, may be broadest near the base, (in most specimens), or as far anteriorly as midlength.

The female from the Strait of Makassar, Indonesia, cited in "Material", was made available to me

FIGURE 12.—*Pseudaristeus crassipes*: *A*, ♀ 35 mm CL, off Djibouti, Gulf of Aden. *B*, ♀ 35 mm CL, Gulf of Mannar, India. Thelyca. Scale = 2 mm.

through the kindness of A. Crosnier, who discussed this shrimp in his work of 1984. He pointed out features that he believed would distinguish it from *P. crassipes* and *P. sibogae*: the absence of setae from the integument; a narrower median plate on sternite XIII (Fig. 13); the absence of setae on the pereopods [typically present in *P. sibogae* but lacking in *P. crassipes*]; and a robust optic calathus which resembles that of *P. crassipes*.

The Indonesian specimen definitely does not belong to *P. sibogae*, but its relation to *P. crassipes* is not entirely clear. A few specimens of the latter species are glabrous, a condition, as noted by Crosnier, unlikely to have been attained accidentally, but absence of setae is not typical of any species of the genus. Variations in the length/width ratio of the optic calathus of *P. crassipes* embrace that of the Indonesian specimen, the mesial margin length of which is equal to the distal width. The maximum width of the median thelycal plate of sternite XIII in most females of *P. crassipes* ranges from 0.50 to 0.55 its length (in one setose specimen, Figure 12*B*, however, it is only 0.47), whereas the maximum width, 0.45, falls below this range in the Indonesian female. The latter exhibits on the plate of sternite XIV a median ridge that ends in a minute anterior spine, the plate is not produced at either side in an anterolateral hood, and the contour of the median plate on sternite XIII is almost uniformly broad from the base to about midlength. These features differ from those of typical *P. crassipes* females in which the plate of sternite XIV is unornamented, a well-developed anterolateral hood is produced at either side, and the contour of the median plate on sternite XIII broadens from a narrow base posterior to its midlength, then tapers to its apex (cf. Figs. 12, 13). Additional material from the Indonesian locality, including males, might provide evidence for assigning this form to a new taxon.

Discussion.—The males of *P. crassipes* differ strikingly from those of its congeners in that the ultimate article of the third maxilliped is twisted (forming a strong concavity laterally), conspicuously expanded proximally, weakly to markedly dilated distally, and studded with minute spines ventrolaterally. The petasma differs from that of *P. kathleenae* and *P. gracilis*, the other 2 species for which adult males are known; the dorsolateral lobule is not expanded distolaterally, as it is in the former, and it tapers gently to a broadly obtuse apex instead of narrowing rapidly as it does in *P. gracilis*. Furthermore, the ventral costa turns somewhat abruptly distomesiad rather than forming a gentle,

FIGURE 13.—*Pseudaristeus crassipes*, ♀ 35 mm CL, Strait of Makassar, Indonesia. Thelycum. Scale = 2 mm.

sinuous curve or simple arc, and, in contrast to the costa of *P. gracilis*, its terminal part, which is also truncate as it is sometimes in the latter species, is not set off by a conspicuous constriction.

The females of *P. crassipes* can be distinguished readily from those of *P. kathleenae* by the shape of the third article of the antennular peduncle, which in the former is uniform in width proximally and tapers distomesially, but in the latter is expanded laterally in a broadly rounded prominence. Also, although the thelyca of these 2 species exhibit a marked resemblance, the median plate of sternite XIII is narrower in *P. crassipes* than that in *P. kathleenae*, its maximum width ranging from 0.45 to 0.55 instead of 0.67 to 0.75.

Remarks.—In the original description of *Aristeus crassipes*, Wood-Mason (1891) cited two females, one from *Investigator* station 116 and another taken at lat. 6°29′N, long. 79°34′E [off southeastern Sri Lanka], perhaps collected by the *Investigator*. He did not designate either specimen as the holotype and consequently they must be considered syntypes. Later, Alcock (1901b) recorded the registration numbers of the various lots of specimens of this

species in the Zoological Survey of India, and next to the number 6713/9, corresponding to the first female cited by Wood-Mason, he added "Types of the species". Immediately following it is the registration number, 3175/9, of the second female (Maya Deb fn. 2). Alcock's referral to "Types" indicate that he did not intend to select the first female as a lectotype; moreover, since he did not specifically designate it as such, according to the Article 74a of the International Code of Zoological Nomenclature of 1961 it cannot be so considered. Maya Deb has also informed me that the female from *Investigator* station 116 is in the Zoological Survey of India accompanied by the registration number cited above, but that the other female recorded by Wood-Mason could not be located. Because two other species, *P. kathleenae* and *P. protensus*, have been confused with *A. crassipes* and conceivably because the missing syntype might prove to be conspecific with one of them, I hereby designate the female in the Zoological Survey of India assigned registration number 6713/9 as the lectotype of *Aristaeus crassipes* Wood-Mason, 1891.

Through the kindness of Maya Deb and H. C. Ghosh, both of the ZSI, who examined the lectotype and provided me with information on specific morphological features, clear drawings, and photographs, I have been able to ascertain the identity of *P. crassipes*. As stated above, the characters used by Wood-Mason in the description of *P. crassipes* were inadequate for distinguishing it from 2 other species and this deficiency was no doubt responsible for the assignments of closely allied forms to *P. crassipes* (De Man 1911, 1913; Kemp and Sewell 1912; Balss 1925). Kemp and Sewell, however, noted that among males of *P. crassipes* in the ZSI there were two types of third maxillipeds which they described and illustrated. They stated further that it was possible that the males exhibiting one of the maxilliped types should be recognized as belonging to a new variety. The "new variety" is described herein as *P. kathleenae*.

Pseudaristeus protensus, new species

Figures 4*D*, 9, 14

Material.

Holotype: ♀, USNM 42681, 40 mm CL, length of median plate of sternite XIII 7.1 mm, basal width 1.5 mm; type-locality W of Evēral Gujārat, India (Arabian Sea); 19°51′30″N, 69°07′30″E; 1,569 m; sand and mud; 14 April 1906; *Investigator* stn 370.

Paratype: ♀, MP, off Godavar, India; 869 m; *Investigator*.

Diagnosis.—Optic calathus relatively short, mesial margin length equal distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle in females not expanded laterally. Pereopods not covered with minute setae. Petasma unknown. Thelycum with plate of sternite XIV very short and produced in long anterolateral hoods; median plate of sternite XIII very long (almost reaching spine on sternite XII), narrow (maximum width 0.40 length), and not expanded posterolaterally in conspicuous prominences.

Description.—Body of holotype and paratype (only two specimens available) slender, studded with minute setiferous punctations and extremely minute setae. Rostrum broken. Anntenal spine broken; branchiostegal spine long, slender, and acutely pointed. Cervical sulcus crossing or just reaching postrostral carina at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt except for sharp, strongly arched ventral extremity; postcervical sulcus deep, almost reaching, but not crossing, postrostral carina at about 0.70 CL from orbital margin, and considerably extending anteriorly. Postrostral carina, extending to 0.85 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus, where turning obliquely almost ventrally forming small branch nearly reaching branchiostegite; branchiocardiac sulcus, accompanied by sharp carina, deep and long, extending posteriorly to near margin of carapace; strong, arched ridge (disposal dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by deep groove, latter continuous posteriorly with postcervical sulcus but not extending anteriorly to cervical sulcus.

Eye (Fig. 4*D*) with optic calathus relatively short, length of mesial margin equal width of distal extremity; mesial tubercle strong and situated at distal 0.33 length of mesial margin.

Antennular peduncle with stylocerite produced in sharply pointed spine almost reaching or falling

short of mesial base of well-developed, sharp, distolateral spine; third article not produced laterally; dorsal flagellum extending to distal 0.2 of scaphocerite; ventral flagellum although incomplete, long, and straight, not mesially curved (concave) just distal to apex of dorsal flagellum.

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length, strong lateral rib ending in acutely pointed small spine falling considerably short of distal end of lamella. Antennal flagellum broken.

Third maxilliped with ultimate article slender but slightly broadening mesially from narrow base, then tapering gently to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad, depressed merus armed with small, slender, distomesial spine.

Abdomen with sharp dorsomedian carina extending full length of fourth somite through sixth, and produced in spine on posterior margin of last 3 somites; sixth somite also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus shallow anteriorly, indistinct posteriorly, and flanked by paired longitudinal dorsolateral ridges (posterior part of telson lacking in types). Lateral ramus of uropod surpassing mesial ramus by about 0.3 its own length.

Thelycum (Fig. 14) with setose plate of sternite XIV very short, deeply excavate transversely, bearing small anteromedian notch, and produced at either side in elongate anterolateral hood; fossa immediately anterior to plate very short and armed with pair of small, oblique lateral ridges. Median plate of sternite XIII very long (length 4.5-4.9 times basal width), narrowly lanceolate (maximum width 0.4 length), strongly produced in sharp apical spine, almost reaching anteromedian spine on sternite XII and covered by very thickly set setae; posterolateral margins of plate raised in slender ridges merging with similar ones extending posteromesially before curving laterally following margin of sternite XIII. Sternite XII minutely setose, strongly raised and bearing low median carina ending anteriorly in minute spine.

Geographic and bathymetric ranges.—Known only from the type-locality, located in the Arabian Sea, and from off Godavari, in the Bay of Bengal, at depths of 1,569 and 869 m respectively (Fig. 9).

Discussion.—Like *P. crassipes*, *P. kathleenae*, and *P. gracillis* but unlike *P. sibogae*, the anterodorsal extremity of the groove dorsal to the posterior part of the hepatic sulcus does not join the cervical sulcus in *P. protensus*; the optic calathus is relatively short, and the pereopods are not covered by setae. *Pseudaristeus protensus* differs strikingly from all its cogeners in several distinctive thelycal features: the plate of sternite XIV is short, bears a small median notch on the anterior margin, and is produced in long anterolateral hoods; the median plate of sternite XIII is very long (4.5-4.9 times the basal width, rather than 1.8-3.5), almost reaching the anteromedian spine on sternite XII, and narrower (maximum width 0.40 instead of 0.45-0.75) than its length. Moreover, it is very densely setose (more so than in its cogeners) and bears a pair of very conspicuous, vertically directed posterolateral ridges.

Although I have examined only two specimens of *P. protensus*, distinct thelycal differences between this gamba prawn and those of other members of the genus leave no doubt that it represents a new species.

Etymology.—Latin *protensus*, stretched forth, referring to the unusual length of the thelycal plate of sternite XIII.

FIGURE 14.—*Pseudaristeus protensus*, n. sp., holotype ♀ 40 mm CL, west of Evēral Gujārat, India. Thelycum. Scale = 2 mm.

Pseudaristeus gracilis (Bate 1888)

Figures 4*B*, 9, 15-17

Hemipenaeus gracilis Bate 1888:302, pl. 44, fig. 2 [syntypes 3 ♂ 3 ♀, BMNH; type-locality: off Tablas I, Philippines; 12°21′N, 122°15′E; 1,240 m; blue mud; 16 January 1975; *Challenger* stn 207]. De Man 1911:26. Estampador 1937:493. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Hemipeneus gracilis. Faxon 1895:198.

Pseudaristeus gracilis. Crosnier 1978:76, fig. 27 bis. 30e.

Material.

Philippines—8 ♀, USNM, Iligan Bay, northern Mindanao; 8°15′20″N, 123°57′E; 750 m; gray mud, sand; 7 August 1909; *Albatross* stn 5511. 1 ♀, USNM, Iligan Bay, northern Mindanao; 8°34′48″N, 124°01′24″E; about 1,280 m; 8 August 1909; *Albatross* stn 5515. 1 ♂, USNM, Macajalar Bay, northern Mindanao; 8°41′30″N, 124°35′40″E; 1,013 m; green mud, fine sand; 4 August 1909; *Albatross* stn 5499. 1 ♂ 2 ♀, USNM, eastern Mindanao Sea; 9°06′30″N, 125°00′20″E; 1,785 m; gray mud; 2 August 1909; *Albatross* stn 5495. 1 ♀, USNM, N of Siquijor I; 9°12′45″N, 123°45′30″E; 1,472 m; green mud, globigerina; 11 August 1909; *Albatross* stn 5526. 1♀, USNM, eastern Mindanao Sea; 9°12′45″N, 125°20′E; 1,344 m; gray mud; 1 August 1909; *Albatross* stn 5492. 1 ♀, USNM, between Bohol and Siquijor Is; 9°22′30″N, 123°42′40″E; 719 m; globigerina ooze; 11 August 1909; *Albatross* stn 5527. 2 ♂ 1 ♀, USNM, eastern Mindanao Sea; 9°24′N, 125°12′E; 1,346 m; green mud, coral; 1 August 1909; *Albatross* stn 5491. 1 ♀, USNM, off Panaon Is, S of Leyte; 9°58′00″N, 125°07′40″E; 1,417 m; green mud; 10 April 1908; *Albatross* stn 5203. 2 ♀, USNM, Sogod Bay, southern Leyte; 10°N, 125°06′45″E; 1,412 m; green mud; 31 July 1909; *Albatross* stn 5488. 1 ♂, USNM, Sogod Bay, southern Leyte; 10°02′45″N, 125°05′33″E; 1,339 m; green mud; 31 July 1909; *Albatross* stn 5487. 1 ♂ 1 ♀, ZSI, Sogod Bay, southern Leyte; 10°10′00″N, 125°04′15″E; 1,013 m; gray sand, mud; 10 April 1908; *Albatross* stn 5201. 2 ♀, MP, SW of Tablas I; 12°09′N, 122°14′E; 1,404 m; 6 June 1985; MUSORSTOM III, stn CP 136. 3 ♂ 3 ♀ syntypes. 1 ♀, MP, SE of Bondoc Point, Luzon; 13°02′08″N, 122°37.1′E; 1,030-1,190 m; 25 November 1980; MUSORSTOM II stn 39. 3 ♂ 3 ♀, MP, NE of Bondoc Point, Luzon; 13°23.2′N, 122°20.7′E; 820-760 m; 26 November 1980; MUSORSTOM II stn 44.

Diagnosis.—Optic calathus relatively short, mesial margin 1.0-1.3 times distal width. Anterolateral carina lacking. Ventral extremity of cervical carina forming sharp-edged arc. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum sinuous and ultimate article of third maxilliped straight and slightly broadening proximomesially before tapering to apex. Pereopods not covered with minute setae. Petasma with distalmost part of dorsolateral lobule narrowing to subangular apex, and ventral surface studded with minute setae; ventral costa slightly inclined distomesially and contracted just proximal to spatulate or paddlelike terminal process. Thelycum with plate of sternite XIV short and produced in moderately long anterolateral hoods; median plate of sternite XIII relatively short (not nearly reaching spine on sternite XII), broad (maximum width 0.80-0.93 length), thickened and expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males short, its length 0.25-0.30 CL and tapering gradually to sharp apex; in females long, 0.90-1.50 CL, relatively deep and convex basally, styliform and slightly upturned anteriorly. Rostral plus epigastric teeth 3; rostral teeth situated variably in males, basally in females. Adrostral carina strong, in males almost reaching apex of rostrum, in females extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostral carina (rarely only reaching it) at about 0.45 CL from orbital margin, ventral part turning anteriorly; accompanying carina blunt, except for sharp, strongly arched ventral extremity; postcervical sulcus reaching, but not crossing, postrostral carina at about 0.7 CL from orbital margin. Postrostral carina, extending to 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by carina, deep and long, extending posteriorly to near margin of carapace; blunt arched ridge, disposed dorsal to posterior part of hepatic sulcus and anterior part

of branchiocardiac sulcus, delimited dorsally by very shallow, sometimes indistinct, groove.

Eye (Fig. 4*B*) with optic calathus relatively short, length of mesial margin 1.0-1.3 times distal width; mesial tubercle strong and variably situated between 0.15 and 0.35 length of mesial margin from base of cornea.

Antennular peduncle with stylocerite produced in sharply pointed slender spine falling distinctly short of, or almost reaching, mesial base of distolateral spine; latter acutely pointed. Third article never produced laterally (Fig. 15*A*); dorsal flagellum about 0.4 length of antennular peduncle, reaching between distal 0.2 and terminal margin of scaphocerite; ventral flagellum long (although incomplete in all specimens examined, in one male 20 mm CL it length 3 times CL), uniquely sinuous, slightly broadened just distal to apex of dorsal flagellum and bearing narrow band of densely set small setae on mesial margin of broadened part (Fig. 15*A*).

Scaphocerite extremely long, surpassing antennular peduncle by as much as 0.4 its own length; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete in all specimens examined.

Third maxilliped in males (Fig. 15*B*) with penultimate article subtriangular in cross section, and not produced in distal process; ultimate article slender, slightly broadening mesially from short, narrow base before tapering to apex (sometimes slightly dilated proximal to tip); in females (Fig. 15*C*) penultimate article more slender than in males, ultimate article broadening slightly from narrow base then tapering to blunt apex.

Pereopods not covered with setae; first and second pereopods with broad, compressed merus bearing small, slender, distomesial spine.

Abdomen with dorsomedian carina extending from fourth through sixth somite, carina low on fourth, sharp and somewhat higher posteriorly, and produced in small spine on caudal margin of each somite; sixth also bearing pair of minute postero-

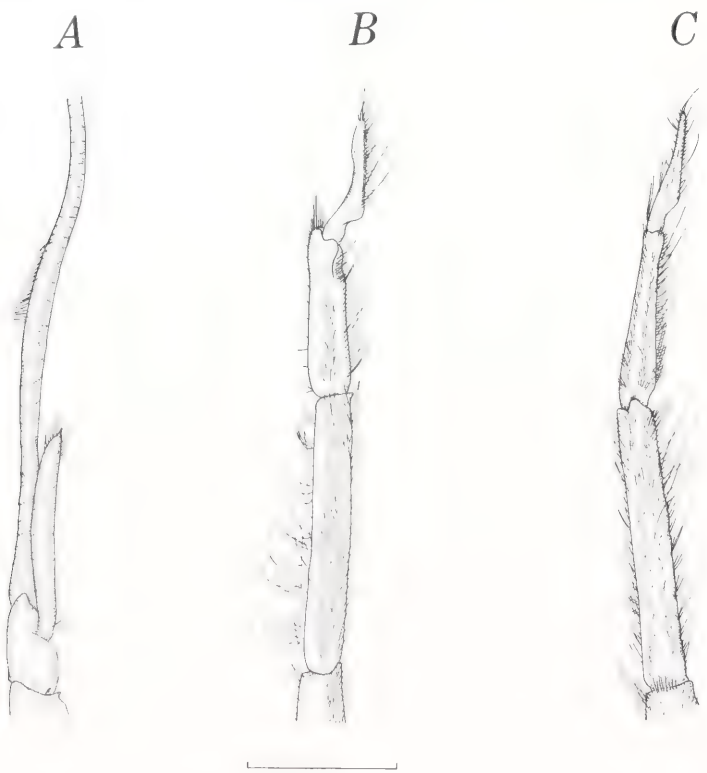

FIGURE 15.—*Pseudaristeus gracilis* (Bate): *A*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines, last article of right antennular peduncle and flagella, dorsal view. *B*, same ♂, distal articles of left third maxilliped, dorsolateral view. *C*, ♀ 35.5 mm CL, between Bohol and Siquijor Islands, Philippines, distal articles of left third maxilliped, dorsal view. Scale = 2 mm.

lateral spines and 2 elongate cicatrices. Telson with median sulcus well defined only on anterior 0.33 length of telson and flanked by paired longitudinal, slender ridges reaching base of third of 4 pairs of movable, marginal spines: 3 situated at about 0.65, 0.80, and 0.90 length from basal margin of telson, fourth flanking short terminal part. Mesial ramus of uropod surpassing apex of telson by about 0.40 its own length; lateral ramus overreaching mesial ramus by about 0.33 its own length.

Petasma in adults (Fig. 16*A*, *B*) with dorsomedian lobule cincinnulate along entire mesial margin. Ventromedian lobule, extending distally as far as dorsolateral lobule, and bearing elongate, lapel-like flap distoventrally along mesial margin. Dorsolateral lobule sclerotized, broad proximally to about base of distal 0.25, then tapering to subacute mesial apex, ventrally bearing conspicuous longitudinal, arched rib and studded with setae. Ventral costa broadly curved along almost entire length, inclined disto-

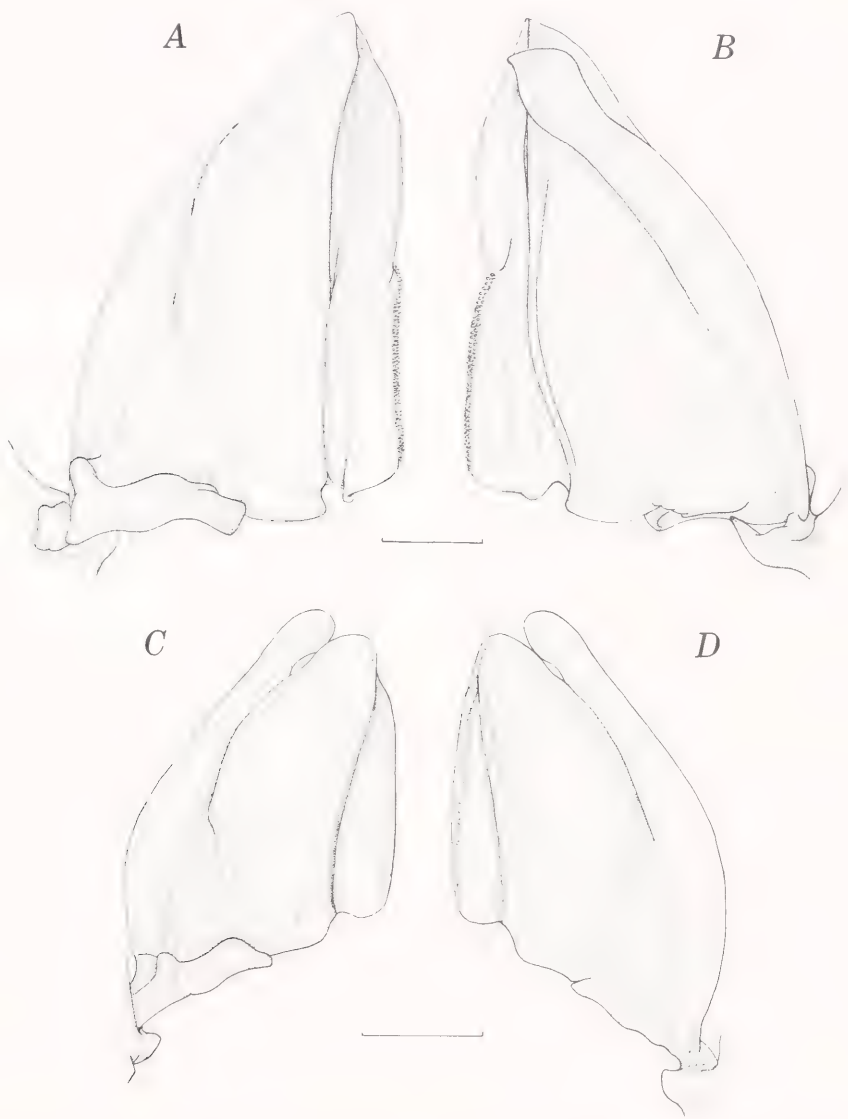

FIGURE 16.—*Pseudaristeus gracilis*, Petasmata: *A*, ♂ 20 mm CL, eastern Mindanao Sea, Philippines, dorsal view of left half. *B*, Ventral view. *C*, Syntype ♂ 13 mm CL, Tablas Island, Philippines, dorsal view of left half. *D*, Ventral view. Scales: *A*, *B* = 1 mm; *C*, *D*, = 0.5 mm.

mesially and with distal part, lying free but against ventral surface of dorsolateral lobule, markedly contracted just proximal to spatulate or paddlelike terminal process.

Petasma in juveniles lacking cincinnuli, specific characters seemingly absent (Fig. 16*C*, *D*): dorsomedian and ventromedian lobules not completely differentiated, but narrow, lapel-like flap present along ventromesial margin; dorsolateral lobule broad proximally, tapering gradually to rounded mesial tip, and with distolateral margin gently curved. Ventral costa arched throughout its length, narrower and contracted distally.

Appendixes masculina and interna as in *P. kathleenae*.

In males, plate of sternite XIV often bearing inconspicuous anteromedian tubercle; plate of sternite XIII flat, roughly lanceolate, produced in sharp spine, its length 1.5-2.3 basal width.

Thelycum (Fig. 17) with densely setose plate of sternite XIV short, deeply grooved transversely, its sharp anteromedian margin turned ventrally, plate produced at either side in moderately long, anterolateral hood; fossa preceding plate long, deep, and bearing pair of small, obliquely disposed ridges. Median plate of sternite XIII, also covered with thickly set setae, concave, and produced apically in acute spine; relatively short (length 2.0-2.7 basal width), falling considerably short of spine on sternite XII, broad (maximum width 0.80-0.93 length), and uniquely expanded in strong posterolateral prominences continuous with slender ridges extending into fossa of sternite XIV. Sternite XII minutely setose, strongly keeled and crested by median carina ending anteriorly in slender, anteroventrally directed spine.

The morphological account above is the first to include adult features. This gamba prawn was named by Bate (1888) on the basis of 6 small juveniles, and the characters pointed out by him have proven inadequate to recognize the species. Subsequent citations to *P. gracilis* have been based only on Bate's information. The material available to me have allowed the detailed descriptions of the petasma, thelycum, and the ventral flagellum of the male which is unique among the members of *Pseudaristeus*.

Maximum lengths.—Males, 21 mm CL; females, 35 mm CL.

Geographic and bathymetric ranges.—Known only from waters of the Philippines (Fig. 9). It has been taken at depths between 719 and 1,785 m.

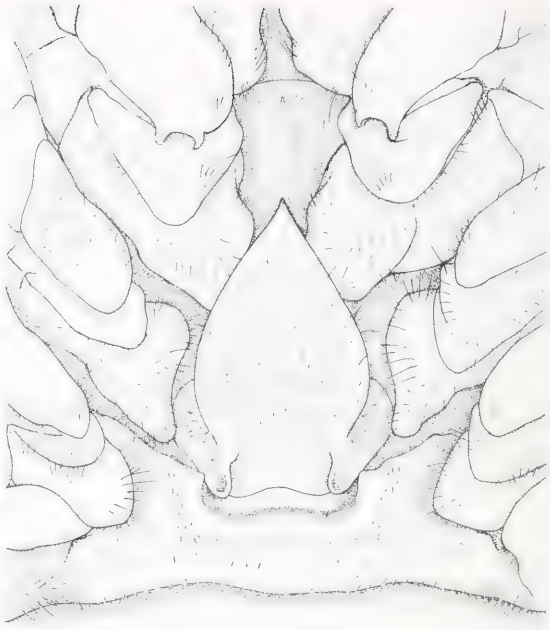

FIGURE 17.—*Pseudaristeus gracilis*, ♀ 35.5 mm CL, between Bohol and Siquijor Islands, Philippines. Thelycum. Scale = 2 mm.

Discussion.—Perhaps the most conspicuous difference between the males of *P. gracilis* and those of the other species of the genus of which males are known is in the ventral antennular flagellum, which is sinuous and bears a dense band of closely set setae on the mesial margin of the slightly broadened part. Males also may be distinguished from those of their cogeners by the shape of the dorsolateral lobule of the petasma, which tapers rapidly to the subangular apex and exhibits a setose ventral surface, and also by the ventral costa, which is markedly contracted distally. Characteristic of the females are the short plate of sternite XIV, in which the anteromedian margin is turned ventrally, and the unique strong posterolateral prominences of the median plate of sternite XIII. The prominences are clearly defined in juveniles as small as the syntype with a 10.3 mm CL.

Pseudaristeus sibogae De Man 1911

Figures 4*E*, 9, 18

Hemipenaeus sibogae De Man 1911:25 [♀ holotype, ZMA De.102.462, E Savu Sea, Indonesia; 9°03′24″S, 119°56′42″E; 1,000 m; globigerina; 20

April 1899; Siboga Exped. stn 52]. De Man 1913, pl. 2, fig. 5, 5a-c. Ramadan 1938:48. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Pseudaristeus sibogae. Crosnier 1978:83, figs. 27a, 30a-c; 1984:22. De Freitas 1985:12, fig. II-5, A-H.

Material.

Madagascar—1 ♀, MP, NW of Ankazomanga; 21°26′30″S, 43°11′00″E; 810-1,020 m; 26 November 1973; *Vauban* stn 92. 1 ♂ 1 ♀, MP, SW of Baie des Assassins; 22°16′48″S, 42°56′00″E; 1,200 m; 30 November 1973; *Vauban* stn 109.

Indonesia—♀ holotype. 1 ♀, USNM, S of Pulau Muna, Sulawesi (Celebes); 5°31′30″S, 122°22′40″E; 834 m; green mud; 16 December 1909; *Albatross* stn 5646. 1 ♂ 2 ♀, USNM, Selat Butung, Sulawesi (Celebes); 5°34′00″S, 122°18′15″E; 950 m; green mud; 16 December 1909; *Albatross* stn 5647. 1 ♀, USNM, off southern Buru; 3°47′15″S, 126°23′40″E; 946 m; fine gray sand; 10 December 1909; *Albatross* stn 5638.

Diagnosis.—Optic calathus long, mesial margin 1.5-1.7 times distal width. Anterolateral carina lacking. Posterior extremity of hepatic sulcus turned ventrally. Third article of antennular peduncle not expanded laterally; males with ventral antennular flagellum never sinuous; ultimate article of third maxilliped straight and slightly broadening proximomesially before tapering to apex. Pereopods covered with minute setae. Adult petasma unknown. Thelycum with plate of sternite XIV moderately long and produced in short anterolateral hoods; median plate of sternite XIII relatively short (not nearly reaching spine on sternite XII) and broad (maximum width 0.60-0.70 length) but not expanded posterolaterally in conspicuous prominences.

Description.—Body slender, densely studded with minute setae. Rostrum in males straight, moderately long, 0.48 and 0.57 CL in 2 specimens, 21 and 22 mm CL, respectively, and roughly lanceolate; in females longer, in one 37 mm CL its length 1.07 CL, rather deep and usually convex, occasionally almost straight basally, styliform and moderately upturned anteriorly. Rostral plus epigastric teeth 3; 2 rostral teeth in males situated at 0.1-0.2 and 0.4 RL respectively, basally in females. Adrostral carina strong, in both males and females extending just anterior to second tooth. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus crossing postrostral carina at about 0.45 CL from orbital margin, with ventral part turning anteriorly; accompanying carina blunt, except for sharp, arched ventral extremity; rather weak postcervical sulcus reaching, but not crossing, postrostral carina at 0.7-0.8 CL from orbital margin. Postrostral carina, extending 0.8-0.9 CL from orbital margin, well marked and sharp to cervical sulcus, low and blunt posteriorly, and followed by small tubercle situated near posterior margin of carapace. Anterolateral carina lacking; gastro-orbital carina strong; antennal carina relatively short; branchiostegal-hepatic carina long, raised and sharp. Orbito-antennal sulcus shallow; deep hepatic sulcus fusing with branchiocardiac sulcus before turning obliquely almost ventrad, forming small branch nearly reaching margin of branchiostegite; branchiocardiac sulcus, accompanied by strong carina, deep and long, extending posteriorly to near margin of carapace; blunt, dorsally concave ridge (disposed dorsal to posterior part of hepatic sulcus and anterior part of branchiocardiac sulcus) delimited dorsally by groove, latter deep and abutting cervical sulcus anterodorsally but becoming shallow posteriorly and indistinct close to postcervical sulcus.

Eye (Fig. 4*E*) with optic calathus long, length of mesial margin 1.50-1.75 times distal width; mesial tubercle small and situated between distal 0.40 and 0.55 length of margin.

Antennular peduncle with stylocerite produced in sharp, slender spine falling conspicuously short to almost reaching mesial base of distolateral spine; latter acutely pointed; third article never produced laterally. Dorsal flagellum about 0.4 length of antennular peduncle, reaching between distal 0.25 and 0.20 of scaphocerite; ventral flagellum long and straight along entire length.

Scaphocerite extremely long, exceeding antennular peduncle by about 0.30-0.35 its own length; strong lateral rib ending in sharp spine falling considerably short of distal margin of lamella. Antennal flagellum broken in specimens examined.

Third maxilliped in both sexes with penultimate article convex dorsally, slightly flattened ventrally, and not produced in distal process; ultimate article also convex dorsally, slightly excavate ventrally, and slender but broadening slightly from relatively elongate, narrow base before tapering to rather blunt apex.

All pereopods covered with minute setae. First and second pereopods with compressed merus bearing distomesial spine.

Abdomen with dorsomedian carina extending from fourth through sixth somites, carina quite low

but clearly distinct on anterior part of fourth, sharp and rather high more posteriorly, and produced in short but strong spine on caudal margin of each somite; sixth also bearing pair of minute posteroventral spines and 2 elongate cicatrices. Telson with median sulcus weak, usually limited to anterior half, flanked by paired longitudinal ridges reaching base of second of 4 pairs of movable, marginal spines situated at about 0.55, 0.75, 0.85, and 0.90 length from basal margin. Mesial ramus of uropod surpassing apex of telson by as much as 0.40 its own length; lateral ramus overreaching mesial ramus by as much as 0.33 its own length.

Petasma of young individual lacking cincinnuli, similar to juvenile petasma of *P. gracilis*. Petasma of adults unknown. Curiously, only male available 21.5 mm CL with petasma still quite undeveloped.

Appendices masculina and interna as in *P. kathleenae*.

In small juvenile males, sternite XIV bearing large, minutely setose prominence, semicircular in outline; median plate of sternite XIII setose, elongate (length 2-3 times basal width), and produced in conspicuous apical spine.

Thelycum (Fig. 18) with setose, moderately long plate of sternite XIV broadly depressed and produced at either side in short anterolateral hood, anteromedian margin varying from weakly convex to concave or biconcave; fossa preceding plate relatively short and bearing pair of small, oblique ridges. Median plate of sternite XIII, also covered with setae, relatively short (length 1.8-2.1 times basal width), falling considerably short of anterior margin of sternite XII; broadly lanceolate (maximum width 0.60-0.70 length), produced apically in acute spine, and flat or slightly excavate; posterolateral margins of plate, lacking bosses, abutting slender ridges extending posteromesially before curving laterally on margin of sternite XIII. Sternite XII minutely setose, strongly convex and crested by slender median carina ending anteriorly in sharp spine.

Color, orange (Crosnier 1978).

Maximum lengths.—Males, 22 mm CL (only juveniles known; the 33.5 mm CL cited by Crosnier (1978) is a misprint, the specimen is a female); females, 47.5 mm CL.

Geographic and bathymetric ranges.—This species has been found off Natal, South Africa, western Madagascar, and in the waters of Indonesia to southern Buru (Fig. 9). It occurs at depths between 834 and 1,200 m and was also taken in a trawl between 810 and 1,020 m.

FIGURE 18.—*Pseudaristeus sibogae* (De Man), holotype ♀ 34 mm CL, east Savu Sea, Indonesia. Thelycum. Scale = 2 mm.

Discussion.—The minutely setose pereopods and the disposition of the deep groove lying dorsal to the posterior part of the hepatic sulcus, which abuts the cervical sulcus, distinguish *P. sibogae* from all the species previously described. It also is distinctive in having a longer optic calathus, the length of the mesial margin being at least 1.45 times its distal width instead of not more that 1.30. The tubercle of the calathus in *P. sibogae* is almost always situated near its midlength, between the distal 0.4 and 0.6 length of the mesial margin rather than only as far as 0.4 or more often less, except in the eye of *P. protensus* in which it is placed about at midlength. In females of *P. sibogae* the median plate of sternite XIII is shorter, its length 1.8-2.1 times the basal width, than in females of its congeners, in which the ratio is usually more than 2.1; in occasional specimens of *P. gracilis* it is 2, overlapping the highest ratios observed in *P. sibogae*.

As stated above, the petasma of the adult of this species is not known; however, the very large prominence of sternite XIV, present in the 2 males examined, appears to be a diagnostic feature. These specimens are 21 and 21.5 mm CL and, curiously,

their petasmata are still little developed, lacking cincinnuli and apparently exhibiting no specific character. In other species, males of this size may be identified by petasmal features. It seems worth mentioning that in the 2 males of this species examined by me, the rostrum is slightly longer, 0.48 and 0.47 CL, than it is in most of the males of its congeners in which it ranges between 0.25 and 0.45 CL.

De Man (1911) indicated that the rostral teeth were less prominent in the female holotype of *P. sibogae* than in the female of *P. crassipes* (= *P. kathleenae*) available to him, and that they were situated in a horizontal line, whereas in the latter "a line uniting the tips of the teeth appears distinctly arcuate". Actually, the arrangement of the teeth in females with the same carapace length varies slightly between individuals of the same species, they are usually disposed in an arc, including *P. sibogae*, but sometimes they are arranged in an almost straight line. De Man also noted that in the holotype of *P. sibogae* the rostrum is much shorter [RL/CL = 0.75] and less slender than in the female of "*P. crassipes*". Crosnier (1978), on the basis of the comparison of a female 37 mm CL (RL/CL = 1.07) with the holotype, believed that the difference in the length of the rostrum seemed invalid, that in the holotype the rostrum was in the process of being generated after having been broken.

Pseudaristeus speciosus (Bate 1881)

Figure 19

Hemipenaeus speciosus Bate 1881:186 [syntypes 1 ♂ 1 ♀ (BMNH); type-locality: E of Río de la Plata, Argentina; 36°44′S, 46°16′W; 2,650 fm (4,847 m); 2 March 1876; *Challenger* stn 325]. Bate 1888: 303, pl. 37, Fig. 3, pl. 44, fig. 3. Murray 1896: 388. De Man 1911:26. Estampador 1937:493. Anderson and Lindner 1945:301. Burukovsky 1974:48.

Hemipeneus speciosus. Faxon 1895:198.

Material.—Argentina Basin—♂ syntype (BMNH).

Diagnosis.—Optic calathus relatively long, mesial margin 1.4 times distal width. Anterolateral carina present. Ventral extremity of cervical carina broad and blunt rather than forming sharp-edged arc. Third article of antennular peduncle in females not expanded laterally. Posterior extremity of hepatic sulcus extending posteriorly subparallel to branchiocardiac sulcus, instead of turning ventrally. Petasma and thelycum unknown.

Description.—Based on few notes by Bate (1881), my observations of his illustration and examination of the incomplete cephalothorax of the male syntype. Body slender, lacking setae. Rostrum (Fig. 19) in male relatively short, its estimated length 0.40 CL and roughly lanceolate. Rostral plus epigastric teeth 3; rostral teeth situated at about 0.35 and 0.75 from orbital margin. Adrostral carina strong almost reaching apex. Antennal spine sharp; branchiostegal spine longer than antennal, acutely pointed. Cervical sulcus reaching but not crossing postrostral carina at about estimated 0.50 CL from orbital margin and well-marked dorsally; accompanying carina weak, its ventral extremity blunt instead of forming sharp-edged arc; postcervical sulcus reaching, but not crossing, postrostral carina at about estimated 0.70 CL from orbital margin. Postrostral carina well marked and sharp to cervical sulcus, low and blunt posteriorly. Anterolateral carina (ventral to gastro-

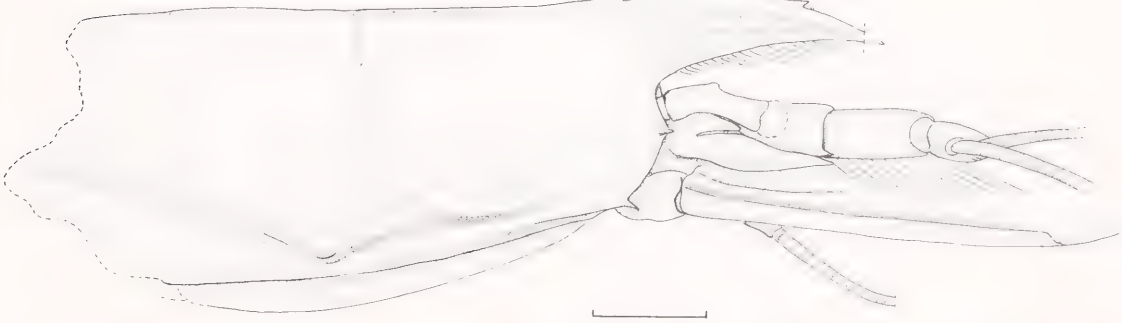

FIGURE 19.—*Pseudaristeus speciosus* (Bate), syntype ♂ "total length = 63 mm" (Bate 1881), off east coast of Buenos Aires. Anterior part of anterior region, lateral view. Scale = 1 mm.

orbital) dorsally concave, rather strong; gastro-orbital carina blunt but well defined; antennal carina relatively short, and branchiostegal-hepatic carina strong and sharp only anteriorly. Orbito-antennal sulcus quite shallow; hepatic sulcus not fusing with branchiocardiac sulcus and extending posteriorly, almost longitudinally rather than turning ventrally, subparallel to anterior part of branchiocardiac sulcus; branchiocardiac sulcus and accompanying carina long, extending posteriorly to near margin of carapace.

Eye with optic calathus relatively long, length of mesial margin 1.4 times distal width; mesial tubercle situated almost at midlength.

Antennular peduncle with stylocerite produced in sharp spine reaching mesial base of distolateral spine; latter small and sharp; third article in females not expanded laterally; dorsal and ventral flagella incomplete.

Scaphocerite long, conspicuously surpassing antennular peduncle; strong lateral rib ending in sharp spine falling considerably short of distal end of lamella. Antennal flagellum incomplete.

Geographic and bathymetric ranges.—*Pseudaristeus speciosus* is known only from the type-locality.

Discussion.—This species, tentatively assigned to the genus *Pseudaristeus*, can be readily distinguished from the other members of the genus in possessing an anterolateral carina; the branchiostegal-hepatic carina is strong and sharp only anteriorly; the ventral extremity of the cervical sulcus is almost straight, instead of turning anteroventrally, and is accompanied by a very weak, rather than sharp, and strongly arched carina; also the posterior part of the hepatic sulcus extends subparallel to the branchiocardiac sulcus instead of fusing with it before turning ventrally.

Pseudaristeus speciosus was described from 2 specimens, one of which is no longer extant and the other has disintegrated except for the anterior part of the carapace to which are attached the eyes, antennules and antennae, and the dismembered distal part of the third maxillipeds. Despite the poor condition of the available syntype, the distinctive features of the carapace, which are clearly represented in Bate's (1888) illustration of the entire animal, are sufficient to conclude that *P. speciosus* is a valid species. Because the branchiae of the syntype are lacking, it is not possible, as noted by Crosnier (1978), to determine with certainty the genus to which it should be assigned, but because of the supraspecific characters exhibited by the carapace, I am almost convinced that it is congeneric with the five Indo-West Pacific species studied herein.

It should be noted that the syntypes of *P. speciosus* were found at 4,847 m, a depth considerably beyond the greatest depth, 1,785 m, at which any of the assumed relatives are known to occur.

ACKNOWLEDGMENTS

Without the generous cooperation of various colleagues this study would not have been possible. I am much indebted to Maya Deb of the Zoological Survey of India for providing descriptions, drawings and photographs of certain morphological features of the lectotype of *P. crassipes*, which permitted a confirmation of the true identity of the species, and for the loan of critical collections from the waters off India; to Alain Crosnier of the Office de la Recherche Scientifique et Technique Outre Mer and the Muséum National d'Histoire Naturelle for his hospitality during a working visit to the latter institution, for the loan of specimens, and for reviewing the manuscript; and to Anthony A. Fincham of the British Museum (Natural History), H.-E. Gruner of the Zoologisches Museum de Humboldt Universitat, and S. Pinkster of the Zoologisch Museum, Amsterdam, for providing materials, including types, from their respective institutions; to H. C. Ghosh of the Zoological Survey of India for a drawing of the antennular peduncle of the lectotype of *P. crassipes*. Horton H. Hobbs, Jr. of the Smithsonian Institution once again offered invaluable advice and innumerable suggestions during the course of my studies and preparation of the paper; Fenner A. Chace, Jr. aided me in solving technical problems and commented on the first draft; Bruce B. Collette and Austin B. Williams of the National Marine Fisheries Service Systematics Laboratory critically read the manuscript. Keiko Hiratsuka Moore, with her artistic talent and devotion to accuracy, made all the illustrations except those of the eyes of various species and the gnathal appendages and of the carapace of *P. kathleenae* which were rendered by María M. Diéguez. Ruth E. Gibbons prepared the map. Virginia R. Thomas and Arleen S. McClain patiently typed several drafts of the manuscript. To all of them goes my deep gratitude.

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DISTRIBUTION AND YIELD OF THE DEEPWATER SHRIMP *HETEROCARPUS* RESOURCE IN THE MARIANAS

ROBERT B. MOFFITT AND JEFFREY J. POLOVINA[1]

ABSTRACT

A shrimp trapping survey was conducted at 22 islands and banks in the Mariana Archipelago during a 2-year field period. Three species of deepwater shrimp were found in abundance at various depths: *Heterocarpus ensifer* at 366-550 m, *H. laevigatus* at 550-915 m, *H. longirostris* >915 m. *Heterocarpus laevigatus* was the largest and most abundant of the three and has the greatest economic potential. Estimates of the unexploited biomass of this species by bank were calculated from estimates of catchability, relative abundance, and habitat area. An archipelago average of the unexploited trappable biomass was estimated to be 0.8 t/nmi^2. Evaluation of length-frequency distributions produced estimates of asymptotic length (L_∞) of 55 mm carapace length, instantaneous growth constant (K) of 0.3 yr^{-1}, and instantaneous total mortality (Z) of 0.75 yr^{-1}. A recommended yield of 162.0 t/year (0.2 t/nmi^2 per year) for the entire archipelago was calculated using the Beverton and Holt yield-per-recruit equation based on minimum spawning stock considerations. Of this yield, 85% would come from the southern islands (e.g., Guam and Saipan), 13% from the northern islands (e.g., Pagan and Anatahan), and 2% from the western seamounts (e.g., Arakane Reef and Pathfinder Reef).

The Mariana Archipelago in the western Pacific Ocean stretches from Guam in the south at lat. 13°N to Farallon de Pajaros (also called Uracas) in the north at lat. 20°N (Fig. 1). Within the approximately 270,000 nmi^2 area of the 200 mi zone around the archipelago are two political entities—the Territory of Guam and the Commonwealth of the Northern Mariana Islands (CNMI)—and three geological formations—the southern island chain, the northern island chain, and the western seamount chain (Karig 1971). The purpose of this study was to assess the standing stock and sustainable yield of the deepwater pandalid shrimp resources in the Marianas.

Pandalid shrimp catches account for about 9% of the world shrimp landings or about 155,000 t in 1982 (FAO 1984). About 98% of this catch is of a few species of the genus *Pandalus* trawled at depths of 70-240 m in the cold-water areas of the North Atlantic, North Pacific, and Bering Sea. The next largest pandalid fishery is the trawl fishery for *Heterocarpus reedi* conducted at depths of 155-424 m in the waters off Chili and Peru (Holthuis 1980). The landings from this fishery were 3,450 t in 1982 (FAO 1984). In recent years, pandalid shrimp resources with commercial potential have been identified from deepwater trapping surveys conducted at depths of 200-1,200 m in the central and western Pacific (Clarke 1972; Wilder 1977; King 1980, 1981a, 1981b; Moffitt 1983). The primary component of these catches has been species of the genus *Heterocarpus*, including *H. laevigatus*, *H. ensifer*, *H. sibogae*, *H. longirostris*, and *H. gibbosus*. Trawling for these species has produced poor results (Struhsaker and Yoshida 1975) which may be due to the depths involved, the rough bottom surrounding the Pacific islands, or behavioral characteristics of the shrimp. In Hawaii a rapidly expanding commercial trap fishery has been established with 1983 annual landings of about 135 t. Catches of 1,350 t have been projected for the near future by the Western Pacific Regional Fishery Management Council (WPRFMC 1984). This projected yield has not materialized and does not appear to be forthcoming since the larger shrimp trapping vessels have left the fishery for economic reasons. Commercial ventures in Guam and the CNMI have been sporadic and short lived; landings of 0.3 t were reported in 1982, the last year that the resource was fished.[2]

SAMPLING GEAR AND METHODS

Shrimp trapping operations in the Mariana Archi-

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[2]Western Pacific Fishery Information Network data on file at the Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

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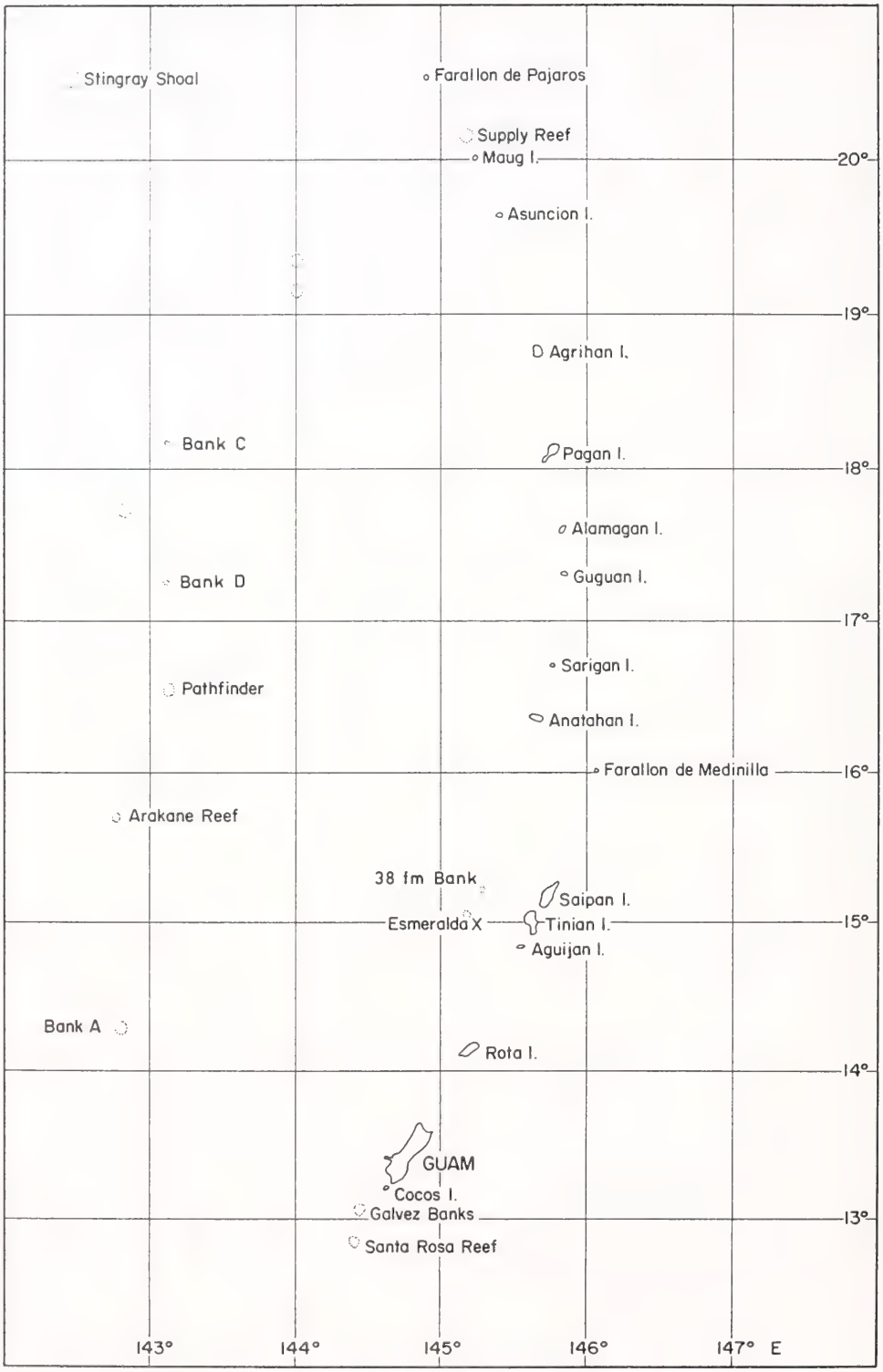

FIGURE 1.—Chart of the Mariana Archipelago.

pelago were conducted on seven cruises of the NOAA ship *Townsend Cromwell* (TC) between April 1982 and August 1984 and one charter cruise of the University of Guam vessel *Pesquedot* (PQ) in August 1984. The standard gear used consisted of strings of five canvas-covered, half-round shrimp traps set about 40 m apart. The traps were constructed of a reinforcing bar frame (about 90 cm long, 65 cm wide, and 45 cm high) wrapped with 2.5 × 1.3 cm mesh, 18-gauge welded wire. An entry cone with an opening of approximately 10 cm was located at each end of the trap. A figure of this general trap design is shown in Gooding (1984). The ground lines attaching the traps together and the main lines attaching the ground line to the surface buoys were of 13 mm polypropylene line. Strings were usually set in the afternoon and retrieved the following morning. Normal soaking times ranged from 15 to 24 hours. Traps were baited with Pacific mackerel, *Scomber japonicus*.

Ordinarily, subsamples of 100 specimens of each of the three major species of *Heterocarpus* (*H. laevigatus*, *H. ensifer*, and *H. longirostris*) were saved each day from each depth sampled. Two sampling sites, Esmeralda Bank and Pagan Island, were visited on each of six *Cromwell* cruises and large subsamples of 400 *H. laevigatus* were saved on each visit. All specimens were returned to the laboratory where the carapace length, sex, and reproductive condition were recorded. The areas of suitable habitat for *H. laevigatus* at each island and bank location was estimated from charts using a computer aided planimeter.

In this study, the yield assessment approach described by Polovina and Ralston (1986) was employed. A systematic survey of 22 islands and banks gave information on the depth range of the primary species and their relative abundance by area. An intensive fishing experiment produced an estimate of catchability using the Leslie method (Ralston 1986). This information combined with an estimate of the area of suitable habitat for each island or bank was used to estimate available biomass by location. Estimates of growth were obtained by application of Elefan I (Pauly 1982) to a site specific time series of length-frequency data. The ratio of mortality to growth and asymptotic length was estimated from a large length-frequency sample (Wetherall et al. in press). Equilibrium yield as a function of fishing mortality was determined from the Beverton and Holt (1956) yield-per-recruit equation as the product of yield per unexploited trappable biomass and the trappable recruited biomass estimate obtained from the systematic sampling and intensive fishing (Polovina and Ralston 1986). Estimates of recommended yield from the equilibrium yield equation were obtained based on marginal yield and minimum spawning stock biomass considerations.

RESULTS[3]

Throughout the course of this survey a total effort of 2,508 trap-nights was expended at 527 shrimp trapping stations. The total catch of pandalid shrimp was 5,188 kg for an overall catch rate of 2.07 kg/trap-night. Over 99% of this catch was composed of *H. ensifer*, *H. laevigatus*, and *H. longirostris*. A complete list of shrimp species taken during this study is given in Table 1.

TABLE 1.—List of shrimp species taken (C = common, F = frequent, R = rare).

Species	Frequency	Depth of abundance (m)
Pandalidae		
Plesionika serratifrons	C	90-270
Plesionika longirostris	C	180-360
Plesionika ensis	F	450-630
Plesionika martia	R	360-450
Heterocarpus ensifer	C	360-540
Heterocarpus gibbosus	R	360-450
Heterocarpus sibogae	R	630
Heterocarpus lepidus	F	540-720
Heterocarpus laevigatus	C	540-810
Heterocarpus dorsalis	F	630-900
Heterocarpus longirostris	C	>900
Heterocarpus tricarinatus	R	900
Oplophoridae		
Acanthephyra eximia	F	810-990
Aristaeidae		
Plesiopenaeus edwardsianus	R	630-810

DEPTH AND SIZE DISTRIBUTION

A plot of catch per unit effort (CPUE) versus depth for the three major species (Fig. 2) shows that they inhabit different depth strata. *Heterocarpus ensifer* is the shallowest dwelling of these species. The maximum catch rate for this species was 0.17 kg/trap-night at a depth of 366 m (200 fathoms). Unfortunately, 366 m was the shallowest depth targeted throughout most of the survey. A small amount of effort was expended in the 137-274 m (75-150 fathoms) depth range on cruises TC-84-02 and PQ-84-01. *Heterocarpus ensifer* catches in this depth range were negligible (only five shrimp in 37 trap-nights). *Heterocarpus laevigatus*, the most abundant shrimp taken in our survey, was caught

[3]Portions of this section are also presented in Polovina et al. 1985.

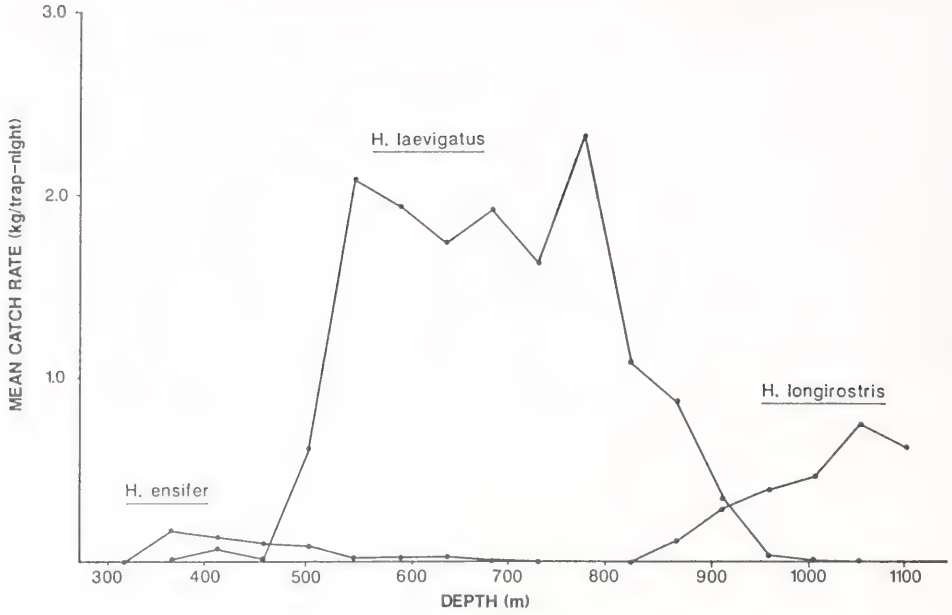

FIGURE 2.—Catch rate of three species of *Heterocarpus* by depth.

in large numbers at depths between 549 and 777 m (300 and 425 fathoms). A maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. *Heterocarpus longirostris* was the deepest dwelling of the *Heterocarpus* species taken, ranging from 823 m (450 fathoms) down past 1,097 m (600 fathoms), which was the greatest depth targeted in this study. Maximum catch rates of *H. longirostris* were obtained at 1,052 m (575 fathoms), but the deeper end of this species' range was not sampled and, as with *H. ensifer*, it is uncertain that the depth of maximum catch rate obtained here is indicative of depth of maximum abundance.

Heterocarpus ensifer was the smallest of the three major species taken. Carapace lengths of 3,401 individuals ranged from 11 to 38 mm with a mean of 26.4 mm. *Heterocarpus laevigatus* was the largest species taken. The mean carapace length was 38.2 mm and the range was 13 to 61 mm (N = 16,405). The mean carapace length of *H. longirostris* was similar to that of *H. laevigatus* ($\bar{x}$ = 37.5 mm), but the size range of 1,443 individuals was more restricted (20 to 50 mm). The mean size of *H. longirostris* taken in this study is probably higher than the mean of catchable shrimp of this species for all depths. We set traps only in the shallower end of this species' depth range (<1,143 m) where the population is dominated by females that grow to a larger size than the males.

It has been suggested that the size of shrimp varies with depth, i.e., larger shrimp occur within the range of maximum abundance while smaller individuals were found in shallower or deeper water (Clarke 1972; Wilder 1977). This type of distribution was not observed for any of the three major species of *Heterocarpus* in the Marianas. Linear regressions of mean carapace length with depth by sex were computed for each of the three species. A significant decrease in carapace length with increasing depth was obtained for *H. longirostris* females, although the full depth range of this species was not sampled. In all other cases, no significant change in size with depth was observed (Table 2).

Wilder (1977) reported high male to female ratios of 3-4 to 1 for *H. ensifer* and *H. laevigatus* taken around Guam. He also stated that small individuals were nearly all males and large individuals almost all female. This was not true for the shrimp examined in this study. The overall sex ratios (ex-

TABLE 2.—Results of mean carapace length by depth regressions for three species of *Heterocarpus* by sex.

Species	Sex	Regression coefficient	R^2	Probability
H. ensifer	Male	0.008	0.41	0.06
	Female	0.002	0.03	0.64
H. laevigatus	Male	−0.007	0.26	0.06
	Female	−0.017	0.16	0.16
H. longirostris	Male	−0.004	0.02	0.83
	Female	−0.04	0.67	0.02

pressed in percent males) for the three major species were 52.8% for *H. ensifer* (N = 3,302), 55.2% for *H. laevigatus* (N = 12,555), and 24.2% for *H. longirostris* (N = 1,408). These ratios tended to hold true for all size classes except the very largest of each species which were indeed nearly all females. Sex ratios did differ by depth showing that the two sexes tend to occupy different areas. In all three major species, females were more abundant at the shallower end of the depth range and males at the deeper end (Fig. 3). This relationship is much more obvious for *H. laevigatus* and *H. longirostris* than for *H. ensifer*. For *H. longirostris*, this may explain the small percentage of males taken in this study since the deeper end of the depth range of this species was not sampled.

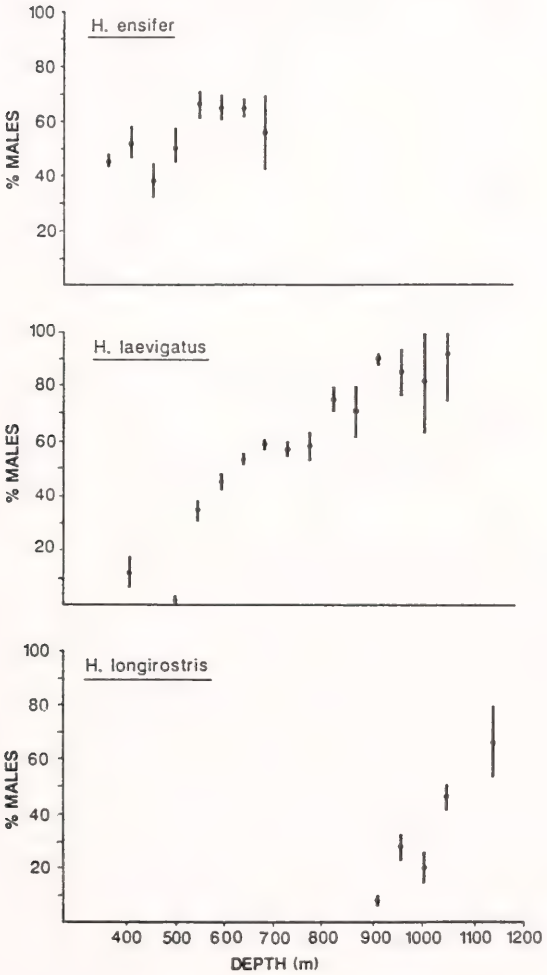

FIGURE 3.—Sex ratio by depth for three species of *Heterocarpus* with 95% confidence limits.

REPRODUCTION

Pandalid shrimp are typically considered to be protandrous hermaphrodites. This is indeed the case for the *Pandalus* species taken in the subarctic areas (Butler 1964). In these species the shrimp spend the first few years of life as functional males, transforming into functional females for the last year or two of life. Clarke (1972) and Wilder (1977) suggested that the tropical *Heterocarpus* shrimp also are protandrous hermaphrodites. The sex ratios obtained in our studies, particularly the near even ratio for the smaller individuals led us to believe that this was not the case. King and Moffitt (1984) examined males of several species of *Heterocarpus* and *Plesionika* for relative growth of the appendix masculina on the second pleopod (a secondary sex characteristic). If these species were indeed protandrous hermaphrodites, the relative size of the male appendage should decrease with increasing carapace length (as the shrimp transforms from male to female). This was not so for any of the tropical pandalids examined. Instead, the relative size of the male appendage increased with increased carapace length indicating maturation as a male. The Marianas data for the ratio (R) of the appendix masculina to the appendix interna versus carapace length (CL) was fit to the logistic model with three parameters, a, b, and c (Gunderson et al. 1980). Table 3 lists the parameters obtained when fitted to the model

$$R \times 100 = \frac{a}{1 + e^{-b(\mathrm{CL}-c)}}.$$

The fit to the nonlinear regression for *H. longirostris* was not particularly good due to the lack of small males in our collection. When the data for this species are fit to a linear regression, however, the slope of the regression is positive indicating relative growth of the secondary sexual characteristics

TABLE 3.—Parameter values for the nonlinear regression of the relative length of the appendix masculina versus carapace length.

Species	a[1]	b	c[2]
Plesionika longirostris	106.83	0.75	11.67
Heterocarpus ensifer	80.35	0.43	15.05
Heterocarpus laevigatus	104.97	0.29	28.09
Heterocarpus longirostris	158.32	0.05	19.36

[1]Asymptotic value for the ratio of the lengths of the appendix masculina and the appendix interna.
[2]Carapace length at the inflection point at 50% of the asymptotic ratio.

with increasing size (regression coefficient = 1.64, r^2 = 0.52).

Based on the assumption that the relative growth of the appendix masculina correlates directly with maturity, we chose the point where this appendage is 90% of its asymptotic value to define the length at maturity for males. The 90% level was used instead of 50% of the asymptotic value, as used for the females below, because the 50% point would be where the males are 50% mature, not where 50% of the males are mature. Using this definition, the carapace length at maturity (L_M) for males of *H. ensifer* is 20.2 mm and that of *H. laevigatus* is 35.7 mm. For *H. longirostris*, the length at maturity is estimated at 31 mm.

The length at maturity of females is perhaps more important in assessment work since the females are directly responsible for the production of recruits to the population. For this study we used the presence of eggs (berried) as the indicator of maturity. The length at maturity is defined as the size where 50% of the females are mature (Gunderson et al. 1980). When using the presence of eggs as the measure of maturity, the sample must be restricted to females collected during the time of year that egg bearing can be expected. For *H. laevigatus*, the breeding season is relatively discrete (November to February), whereas for *H. ensifer* and *H. longirostris* there are peaks in December and May (Fig. 4). Data for each species were fitted to the same nonlinear regression model used for the males. Asymptotic values for percent berried by carapace length are 66% for *H. ensifer*, 92% for *H. laevigatus*, and 55% for *H. longirostris*. The carapace lengths associated with values equal to one-half of the asymptotic values are the L_M for the various species. These are 23.9 mm for *H. ensifer*, 42.7 mm for *H. laevigatus*, and 37.4 mm for *H. longirostris*.

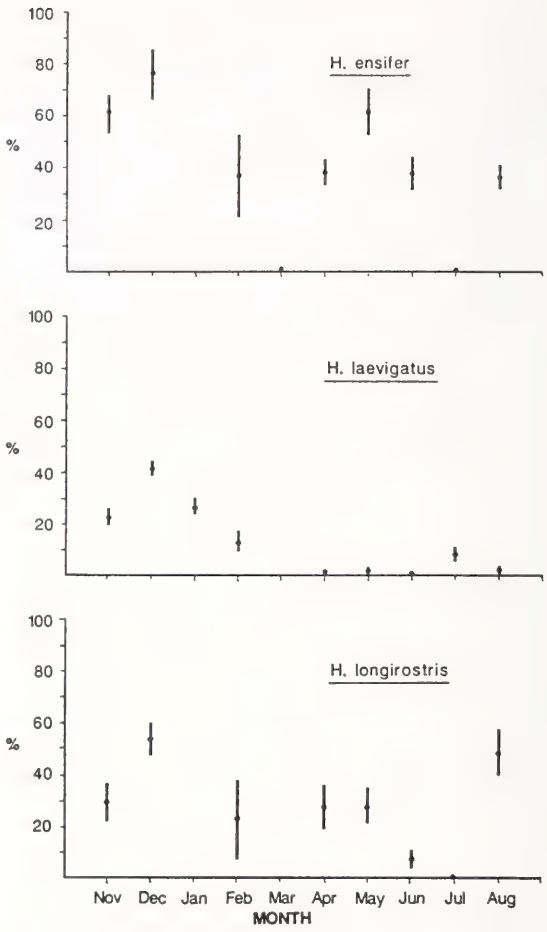

FIGURE 4.—Percentage of females bearing eggs by month for three species of *Heterocarpus* with 95% confidence limits.

YIELD ASSESSMENT

The assumptions and methods of yield assessment used in this study are presented in Polovina and Ralston (1986) and Wetherall et al. (in press). Because *H. laevigatus* yielded the highest catch rates and because it is generally regarded as having superior market acceptability, most of our fishing effort targeted this species. Hence estimates of total biomass and sustainable yield for the pandalid resource are restricted to this species.

GROWTH AND MORTALITY

Estimates of asymptotic size (L_∞) and the ratio of instantaneous total mortality to the instantaneous growth constant (Z/K) were obtained by examining the descending limb of the length-frequency distribution using the regression method based on the Beverton and Holt (1956) model (Wetherall et al. in press). Table 4 lists the values of L_∞ and Z/K for males, females, and pooled sexes for each of the three major species. As anticipated, L_∞ values for females are larger than those for males of the same species. Estimates of length at recruitment to the exploitable population (L_R) were obtained by applying the method of Gulland (1969) to the ascending limb of the same length-frequency distributions. *Heterocarpus ensifer* is recruited into the fishery at a carapace length of 23 mm, *H. laevigatus* at 29 mm, and *H. longirostris* at 34 mm.

By fixing the L_∞ value at the estimates obtained from the large length-frequency sample and using

TABLE 4.—L_∞ and Z/K estimates for the three major species of *Heterocarpus* by sex from length-frequency data.

Species	L_∞	Z/K
Heterocarpus ensifer		
Males	34.5	2.6
Females	37.5	3.0
Sexes combined	36.6	2.9
Heterocarpus laevigatus		
Males	51.3	2.1
Females	55.4	1.9
Sexes combined	55.2	2.5
Heterocarpus longirostris		
Males	41.0	1.7
Females	48.1	1.9
Sexes combined	48.6	2.2

Elefan I (Pauly 1982) to fit the von Bertalanffy growth curve to the time series data for *H. laevigatus* collected at Esmeralda Bank and Pagan Island, the growth constant K can be estimated. When applied to the sexes separately, multiple estimates were obtained for each category ranging from 0.19 to 0.31 yr^{-1}. The inconsistency of these estimates within area and sex groupings was most likely due to the small sample size. When sexes were pooled, however, K was estimated at 0.30 yr^{-1} for both areas. Estimates of the age at recruitment and maturity were obtained by solving the von Bertalanffy equation for the particular carapace lengths estimated above. For female *H. laevigatus*, with a L_R = 29 mm, the T_R = 2.0 years, and with L_M = 43 mm, the T_M = 4.5 years. With a K estimate of 0.3 yr^{-1} and Z/K of 2.5, an estimate for Z of 0.75 yr^{-1} is obtained. Because there is no fishery for *H. laevigatus* in the Marianas, Z is equivalent to natural mortality (M).

UNEXPLOITED BIOMASS

Because standard trapping techniques were used throughout our study, CPUE values from various locations could be used as a measure of relative abundance. The unexploited biomass of the *H. laevigatus* resource for each area is then calculated as the product of the area of suitable habitat and relative abundance divided by the coefficient of catchability (q = 0.001945 trap-night^{-1}) estimated from the Alamagan Island intensive trapping operation (Ralston 1986). Although the catch rate from the western seamounts is about twice that of the southern island chain, the fiftyfold greater area of suitable habitat around the southern islands more than compensates for the low catch rates in producing a higher biomass estimate for the southern islands (Table 5).

TABLE 5.—Catch rates, habitat areas, and unexploited biomass estimates for *Heterocarpus laevigatus* by location.

	Catch rate (kg/trap-night)	Area (nmi^2)	Biomass (t)
Northern Banks			
Maug	1.88	3.83	3.7
Asuncion	2.11	5.93	6.4
Agrihan	1.96	12.39	12.5
Pagan	2.17	16.19	18.0
Alamagan	2.18	11.43	12.8
Guguan	2.52	5.60	7.2
Sarigan	1.45	4.55	3.4
Anatahan	2.36	10.89	13.2
38 Fathom Bank	2.12	6.37	6.9
Esmeralda Bank	1.35	2.03	1.4
Mean =	2.01	Total = 79.21	85.5
Southern Banks			
Farallon de Medinilla	0.97	88.55	44.2
Saipan	2.06	213.99	226.5
Tinian	1.81	73.80	68.4
Aguijan	1.61	39.36	32.6
Rota	1.02	197.31	103.6
Guam	0.48	44.24	16.2
Galvez and Santa Rosa	1.78	50.77	84.5
Mean =	1.39	Total = 708.02	576.0
Seamounts			
Bank C	2.07	2.71	2.9
Bank D	2.72	2.71	3.8
Pathfinder	2.79	2.71	3.9
Arakane	2.83	2.10	2.1
Bank A	1.43	3.33	2.4
Mean =	2.37	Total = 13.56	15.1

EQUILIBRIUM YIELD

With the values for K, L_∞, M, and T_R, the Beverton and Holt yield-per-recruit equation can be used to compute the ratio of equilibrium yield to unexploited recruited biomass (Y/B) as a function of fishing mortality (F) (Polovina and Ralston 1986). Because the shrimp resource in the Marianas is not fished, the estimates of the biomass for each bank represent the unexploited trappable biomass (B), and hence, the product of Y/B and B gives the equilibrium yield as a function of F (Table 6). As F increases, the equilibrium yield increases rapidly for low levels of F. The relationship between F and the equilibrium yield estimated from the Beverton and Holt yield-per-recruit equation assumes that recruitment is unchanged as F increases and does not take into account any economic considerations. Ideally a spawner-recruit relationship is needed to account for changes in yield because of the changes in recruitment which might occur as F increases. However, in the absence of a knowledge of the spawner-recruit curve, two approaches can be used to estimate recommended yield. One approach esti-

TABLE 6.—Equilibrium yield of *Heterocarpus laevigatus* and relative spawning stock biomass as a function of fishing mortality (F).

F	Total yield (t)	Relative spawning stock biomass
0.1	56.2	0.70
0.2	95.6	0.51
0.3	124.2	0.37
0.4	145.4	0.27
0.5	161.6	0.20
0.6	174.1	0.15
0.7	184.1	0.11
0.8	192.0	0.09
0.9	198.5	0.07
1.0	203.8	0.05

mates the recommended yield from the yield-per-recruit derived yield equation as the yield which corresponds to that level of effort where an increase in one unit of effort will increase the catch by 0.1 of the amount caught by the very first unit of effort (Gulland 1983, 1984). This effort is denoted as $F_{0.1}$ and the corresponding yield as $Y_{0.1}$. The value of $F_{0.1}$ for *H. laevigatus* in the Marianas is 0.8 and $Y_{0.1}$ is 192 t annually (Table 6) from areas within the depth range of 500-825 m.

A second approach to estimate recommended yield uses a computation of the spawning stock biomass. With an age estimate of the onset of sexual maturity, the spawning stock biomass for a level of F relative to the spawning stock biomass, in the absence of fishing, can be computed from the Beverton and Holt yield-per-recruit equation (Polovina and Ralston 1986). This relative spawning stock biomass can be used to determine the maximum value of F before a substantial decline in recruitment occurs. The recommended yield can then be estimated as the yield from the constant recruitment yield curve which corresponds to that maximum value of F. This is a conservative approach because it does not incorporate any density dependent compensation, i.e., size at onset of sexual maturity does not decrease as density decreases. The relationship between the relative spawning stock biomass and recruitment is not known for *H. laevigatus*, but it has been suggested that as a lower bound the relative spawning stock biomass should not be reduced below 20% of the unexploited level if a substantial reduction in recruitment is to be avoided (Beddington and Cooke 1983). When F is 0.5, the relative spawning stock biomass is estimated to be 20% of the unexploited level, and the equilibrium yield at this level of fishing is estimated at 162 t annually (Table 6) for the depth range of 500-825 m. To be conservative, the lower yield estimate of 162 t annually from the Mariana Archipelago will be used. Given the habitat area from 500 to 825 m, this yield is equivalent to 0.20 t/nmi^2. An approximate variance for this yield, and hence an approximate confidence interval, can be computed from a Taylor series expansion of the yield estimator if it is assumed that the variance of the yield estimate is due primarily to variances in bank CPUE and catchability. The yield at each bank is computed as

$$\text{Yield} = (\text{CPUE}/q)(\text{Area})(Y/B).$$

Thus the variance of the yield (V(Yield)) can be expressed as

$$V(\text{Yield}) = (\text{Area})^2(Y/B)^2 V(\text{CPUE}/q),$$

$$= (\text{Area})^2(Y/B)^2 \times \left[\frac{V(\text{CPUE})}{q^2} + \frac{(\text{CPUE})^2\, V(q)}{q^4} \right].$$

Estimates of V(CPUE) were obtained from the repeat sampling at each bank and ranged from 0.02 at Guam to 0.64 at Sarigan, while $V(q)$, estimated at 5.5×10^{-7}, was obtained from the intensive trapping work. The variance of the total yield was estimated as the sum of the individual bank variance. The 95% confidence interval, derived from the estimate ± 1.96 times the standard deviation of the estimate of total yield, resulted in a targeted yield range of 102 to 218 t (0.12 to 0.27 t/nmi^2) per year. About 85% of this yield would come from the southern islands and banks, 13% from the northern islands, and about 2% from the western seamounts (Table 7).

DISCUSSION

Although trap design, depth fished, and species present undoubtedly affect catch rate, catch rates reported in other studies using differing trap designs in various areas fall within a fairly tight range of 1.2 to 6.6 kg/trap-night (Table 8). This indicates that the productivity of deepwater pandalids is relatively uniform throughout the tropical central and western Pacific, and the first estimate of recommended yield of 0.2 t/nmi^2 obtained from the Mariana Archipelago can be applied to other Pacific islands, though the relative importance of the various species may differ greatly from area to area.

In our study *H. ensifer*, *H. laevigatus*, and *H.*

TABLE 7.—Equilibrium yield for *Heterocarpus* shrimps in the 500-825 t depth range for a fishing mortality of 0.5.

Bank	Yield (t/yr)
Northern Banks	
Maug	0.9
Asuncion	1.5
Agrihan	3.0
Pagan	4.3
Alamagan	3.0
Guguan	1.7
Sarigan	0.8
Anatahan	3.1
38 Fathom	1.7
Esmeralda	0.3
Total	20.3
Southern Banks	
Farallon de Medinilla	10.6
Saipan	54.1
Tinian	16.3
Aguijan	7.8
Rota	24.7
Guam	3.9
Galvez and Santa Rosa	20.2
Total	137.6
Seamounts	
Bank C	0.7
Bank D	0.9
Pathfinder	0.9
Arakane	0.5
Bank A	0.6
Total	3.6
Archipelago total	161.5

TABLE 8.—Catch rates of pandalid shrimp in the tropical Pacific.

Area	Catch rate (kg/trap-night)	Source
Tonga	1.2	King 1981b
Samoa	1.4	King 1980
Fiji	1.5	King 1983
Hawaii (main islands)	1.5	Clarke 1972
Guam	2.1	Wilder 1977
Mariana Archipelago	2.1	Present study
Hawaii (NWHI)	2.5-3.5	Oishi 1983
Vanuatu	2.8	King 1981a
Hawaii (main islands)	3.5-5.0	Hawaiian Divers, Inc. 1983 (text fn. 4)
Hawaii (main islands)	6.6	Struhsaker and Aasted 1974

longirostris proved to be the major components of the catch within their respective depth zones. *Heterocarpus ensifer* was the shallowest dwelling and the least abundant of the three major species in the Marianas. Its range of abundance was 366 to 503 m (200 to 275 fathoms) and the peak catch rate was 0.17 kg/trap-night at 366 m. In Hawaii, *H. ensifer* appears to be the most abundant species. Average catch rates are between 1.5 and 6.6 kg/trap-night in a somewhat wider reported depth of abundance of 274 to 600 m (Clarke 1972; Struhsaker and Aasted 1974; Gooding 1984). In the Southern Hemisphere; *H. ensifer* is not found in great abundance and is replaced in the 300 to 500 m depth range by a very closely related species, *H. sibogae* (King 1983).

Heterocarpus laevigatus is an important part of the catch throughout the central and western Pacific. In the Marianas, this was the most common species. Its abundance peaked between 549 and 777 m (300 and 425 fathoms) and the maximum catch rate of 2.33 kg/trap-night was obtained at 777 m. In the Northwestern Hawaiian Islands (NWHI), the same standard half-round traps caught just under 1.0 kg/trap-night in an optimum depth range of 500 to 800 m (Gooding 1984). Commercial vessels using larger traps obtained catches of 2.5 to 5.0 kg/trap-night in the Hawaii area and found that the optimum depth range is shallower in the main Hawaiian Islands (530 to 622 m) than in the NWHI (640 to 732 m) (Hawaiian Divers 1983[4]; Oishi 1983; Gooding 1984). In the South Pacific, *H. laevigatus* is reported to be abundant at depths of 549 to 640 m and catch rates range from 0.4 to 1.1 kg/trap-night depending on the area studied (King 1983).

Before this study, *H. longirostris* had been known to science from only four specimens taken in the Indian Ocean (Moffitt 1983). In the Marianas, it occurs in sufficient quantity to suggest a commercial potential. *Heterocarpus longirostris* is probably present in many other areas in the Pacific but has not been found because its optimum depth range is below those sampled.

In the Marianas, sex ratio varied with depth for all three of the major species of *Heterocarpus*. For each species, a larger percentage of the catch is composed of females at the shallower end of the species' depth range. A similar distribution in Hawaii has been reported for *H. ensifer* (Clarke 1972) and *H. laevigatus* (Dailey and Ralston 1986).

Changes in the mean size with depth have been reported for *H. ensifer* and *H. laevigatus*. Wilder (1977) and Gooding (1984) reported increases in size with increasing depth for *H. ensifer* from Guam and the NWHI, respectively. Clarke (1972), on the other hand, found that a higher proportion of larger individuals in Hawaii occupied the depth of greatest abundance, while smaller individuals were found in shallower or deeper water. Gooding (1984) noted a

[4]Hawaiian Divers, Inc. 1983. Deepwater shrimp utilization study for Hawaii. Report prepared under NOAA Cooperative Agreement No. 80-ABH-00065 for the Southwest Region, Western Pacific Program Office, National Marine Fisheries Service, NOAA, 47 p.

decline in size (kilograms/individual) with increasing depth for *H. laevigatus* in the NWHI. In all of these studies, changes in sex ratio with depth were not taken into account. As we have shown, sex ratio does change with depth and the sexes do grow at different rates. The observed changes in size with depth may be due to changes in sex ratio rather than size-specific stratification. Dailey and Ralston (1986) examined the sexes separately and found that for *H. laevigatus* in Hawaii the carapace length of males and egg-bearing females displayed no apparent change with depth, whereas that of nonegg-bearing females showed a strong inverse relationship. In the Marianas, significant changes in mean carapace length with depth were not observed for either sex of the three species of *Heterocarpus*, except for female *H. longirostris* (Table 2). For this group, an inverse relationship was observed much like that found for nonegg-bearing female *H. laevigatus* in Hawaii (Dailey and Ralston 1986).

The estimates of growth parameters for *H. laevigatus* obtained in this study correspond well with those of other authors (Table 9). Using the regression method (Wetherall et al. in press), we estimated L_∞ to be 51.3 mm CL for males, 55.4 mm CL for females, and 55.2 mm CL for the pooled population in the Marianas. Using the same method, Dailey and Ralston (1986) obtained estimates of 57.9 mm CL for males, 62.5 mm CL for females, and 61.7 mm CL for the combined sexes in Hawaii. Apparently, *H. laevigatus* grows about 7 mm larger in Hawaii than in the Marianas. King (1983), using the Beverton and Holt method, estimated L_∞ = 57 mm CL for *H. laevigatus* in Fiji.

Estimates of Z/K for *H. laevigatus* in the Marianas were 2.1 for males, 1.9 for females, and 2.5 for the sexes combined. In Hawaii, Z/K estimates of 4.3, 2.9, and 2.6 were obtained for the same categories, respectively (Dailey and Ralston 1986). The Z/K estimates for the combined sexes are nearly identical in the two studies. In our study, Z/K estimates for the two sexes were similar to each other and lower than that of the sexes combined, whereas in the Hawaii study they were very different from each other and both larger than that of the combined sexes. In our study, if we assume that instantaneous growth of the two sexes is similar, then mortality will also be similar and close to the 0.75 yr^{-1} value estimated for the pooled sexes. In the Hawaii study, Z/K estimates for males and females differed widely. Mortality estimates differed considerably as well, Z = 1.51 yr^{-1} for males and 0.73 yr^{-1} for females.

The K parameter for *H. laevigatus* in the Marianas was estimated as K = 0.30 yr^{-1} for the combined sexes (Table 9). Estimates of K for the individual sexes were ambiguous and inconsistent. King (1983) estimated K as 0.27 yr^{-1} for *H. laevigatus* in Fiji and Dailey and Ralston (1986) estimated K as 0.35 yr^{-1} for male and 0.25 yr^{-1} for female *H. laevigatus* in Hawaii. Because growth estimates for *H. laevigatus* are similar for the various areas studied, it is not surprising that estimates of age at maturity are also similar (Table 9). King (1983) reported the age at maturity for female *H. laevigatus* in the South Pacific as 4.6 years (40.5 mm CL). He further suggests that males mature at about 24 mm CL (age not calculated). Dailey and Ralston (1986) found that females in Hawaii mature at 40 mm or about 4 years. In the Marianas female maturity is estimated at 43 mm CL or about 4.5 years. Males mature earlier at 35.7 mm CL or about 3.0 to 3.5 years. Male maturity estimates by King (1983) and this study are based on the relative growth of the appendix masculina on the second pleopod. King appeared to have chosen 50% of the asymptotic value as the point of maturity much as the point where 50% of the female shrimp are bearing eggs is used to define maturity for females. We feel that 90% of the asymptotic value is a better estimate of male maturity and have used that point in our estimate for the Marianas.

TABLE 9.—Asymptotic length (L_∞), instantaneous growth constant (K), length at maturity (L_M), and age at maturity (T_M) of *Heterocarpus laevigatus*.

Location	L_∞ (mm)	K (yr^{-1})	L_M	T_M
Fiji				
(King 1983)				
Sexes combined	57	0.27		
Females			40.5	4.6
Males			24	
Hawaii				
(Dailey and Ralston 1986)				
Sexes combined	61.7			
Females	62.5	0.25	40	4
Males	57.9	0.35		
Mariana Archipelago				
(present study)				
Sexes combined	55.2	0.30		
Females	55.4		43	4.5
Males	51.3		36	3.5

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DECLINE IN ABUNDANCE OF THE NORTHERN SEA LION, *EUMETOPIAS JUBATUS*, IN ALASKA, 1956-86

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ABSTRACT

Aerial, ship, and onshore surveys were conducted to assess the abundance of northern sea lions, *Eumetopias jubatus*, in southwestern Alaska, from the central Gulf of Alaska through the central Aleutian Islands, during June-July of 1984-86. Counts of northern sea lions from these surveys were compared with counts made in 1956-62 and 1975-79. These data indicated that the number of adults and juveniles onshore declined 52% from 140,000 animals in 1956-60 to 68,000 in 1985—an annual rate of decline of at least 2.7%. Numbers have declined throughout the region, with the greatest declines in the eastern Aleutian Islands (79%) and the least in the central Aleutian Islands (8%). This was not due to emigration because significant increases have not been noted elsewhere. Between the 1960s and mid-1970s, there were large decreases in the eastern Aleutian Islands and western Gulf of Alaska, and a major increase in the central Aleutian Islands. Beginning in the late 1970s declines occurred in all areas. The causes of the declines are unknown, but they may be associated with disease, prey availability or quality, or a combined effect of these and other factors. Factors which may contribute to the declines include the pre-1973 commercial harvests, entanglement of juveniles in marine debris, incidental takes in fisheries, and killing by fishermen.

The northern or Steller sea lion, *Eumetopias jubatus*, breeds from the Kuril Islands and Okhotsk Sea through the Aleutian Islands and Gulf of Alaska, and south to California. Loughlin et al. (1984) estimated the maximal population in 1974-80 at 290,000 (including some pups), of which more than 196,000 were in Alaska. The number of northern sea lions counted in Alaska was unchanged since the surveys of Kenyon and Rice (1961) and Mathisen and Lopp (1963) in 1956-60, even though significant declines had occurred in the eastern Aleutian and Pribilof Islands (Kenyon 1962; Braham et al. 1980). These declines were offset by increases in northern sea lion numbers in the central and western Aleutian Islands (Fiscus et al. 1981).

Concern over the decline in northern sea lion numbers in the eastern Aleutian Islands prompted the National Marine Mammal Laboratory (NMML) and the Alaska Department of Fish and Game to conduct surveys in 1984, 1985, and 1986 at sites throughout southwestern Alaska. These included aerial, ship, and onshore surveys of rookeries and major haul-out sites from Kiska Island in the central Aleutian Islands to the Barren Islands in the central Gulf of Alaska, as well as observations during two breeding seasons at Ugamak Island, a major rookery in the eastern Aleutian Islands. Together with earlier data for the Aleutian Islands (Kenyon and Rice 1961; Kenyon 1962[3]; Kenyon and King 1965[4]; Braham et al. 1980; Fiscus et al. 1981) and for the Gulf of Alaska (Mathisen and Lopp 1963; Calkins and Pitcher 1982[5]), these data present a 30-yr record of counting northern sea lions, albeit sporadically, in Alaska waters. The objectives of this paper are 1) to report the results of surveys conducted between 1984 and 1986, thus describing the current distribution and numbers of northern sea lions in much of Alaska, 2) to compare those counts with the historical data, and 3) to discuss the state of knowledge on causes of the decline in sea lion numbers.

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[4]Kenyon, K. W., and J. G. King, Jr. 1965. Aerial survey of sea otters and other marine mammals, Alaska Peninsula and Aleutian Islands, 19 April to 9 May 1965. Processed Rep., U.S. Fish Wildl. Serv., Bur. Sport Fish. Wildl., Seattle, 52 p. Avaliable from Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115.

[5]Calkins, D. G., and K. W. Pitcher. 1982. Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska. Alaska Dep. Fish and Game, Final Rep. RU243, 128 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

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STUDY REGION AND METHODS

Study Region

The study included northern sea lion hauling sites in southwestern Alaska from Kiska Island in the Aleutian Island chain eastward to the Barren Islands in the central Gulf of Alaska (Fig. 1). This region was subdivided for analysis into four areas: 1) central Gulf of Alaska, 2) western Gulf of Alaska, 3) eastern Aleutian Islands, and 4) central Aleutian Islands.

Two general types of northern sea lion sites on land were recognized—rookeries and haul-outs (Loughlin et al. 1984). Rookeries were areas where adult males actively defended territories and most females gave birth and mated. Haul-outs were sites where few pups were present and where little breeding took place. Some islands included more than one distinct rookery and haul-out. A total of 114 sites, of which 28 were rookeries (on 27 islands), were surveyed during 1984-86.

Ugamak Island was a site for NMML field studies during the northern sea lion breeding seasons in 1969, 1977, 1978, 1985, and 1986. The island is located in the eastern Aleutian Islands (long. 164°50′W, lat. 54°14′N), about 110 km east of Dutch Harbor, AK. The island contained the largest aggregation of breeding sea lions in the Aleutian Islands as late as 1969.

Survey Methods

Aerial photographic surveys of northern sea lion rookeries and haul-outs in the eastern Aleutian Islands area (Fig. 1) were conducted 7-12 July 1984, using a Bell 205[6] helicopter flown off of the NOAA ship *Surveyor*. A survey of the entire study region

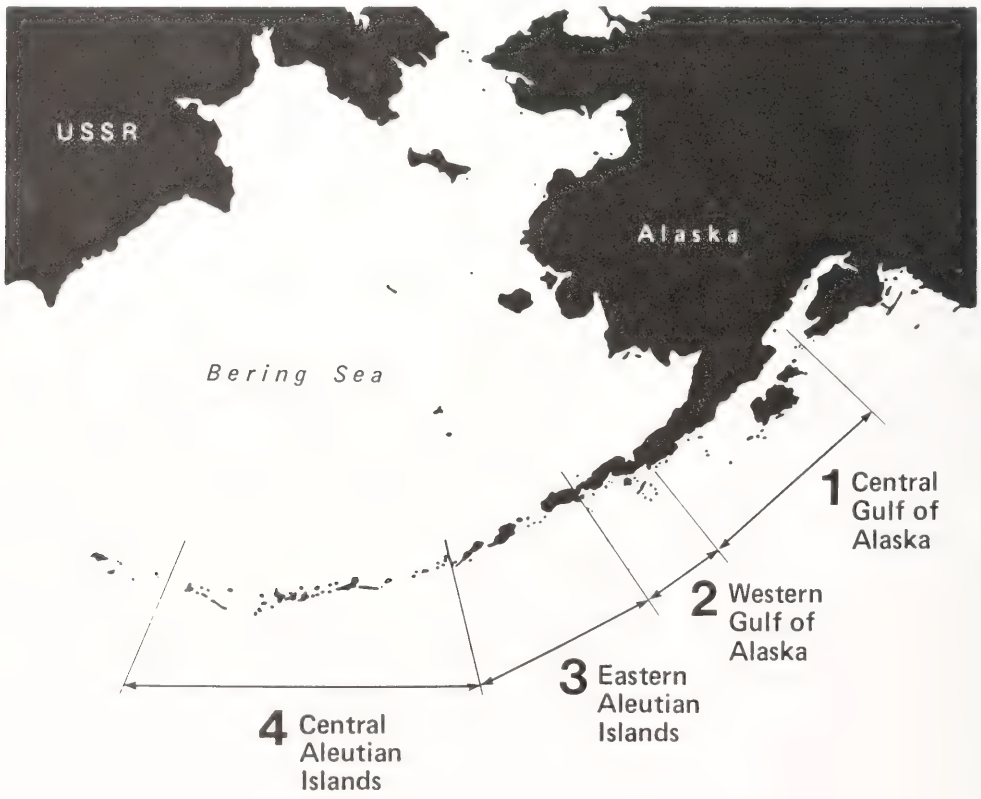


FIGURE 1.—The four Alaskan study areas (left) and 28 northern sea lion rookery sites (right) counted during 1984-86. Rookery island name and number as in Table 2.

was conducted during 9-13 June 1985, using a Grumman Widgeon for the eastern Aleutian Islands and Gulf of Alaska and a Piper Navajo for the central Aleutian Islands. All surveys were conducted between the hours of 1000 and 1800 Alaska Daylight Saving Time (ADT) and from mid-June to mid-July, when the most adult and juvenile sea lions were expected to be onshore (Withrow 1982). Survey methods were those of Braham et al. (1980).

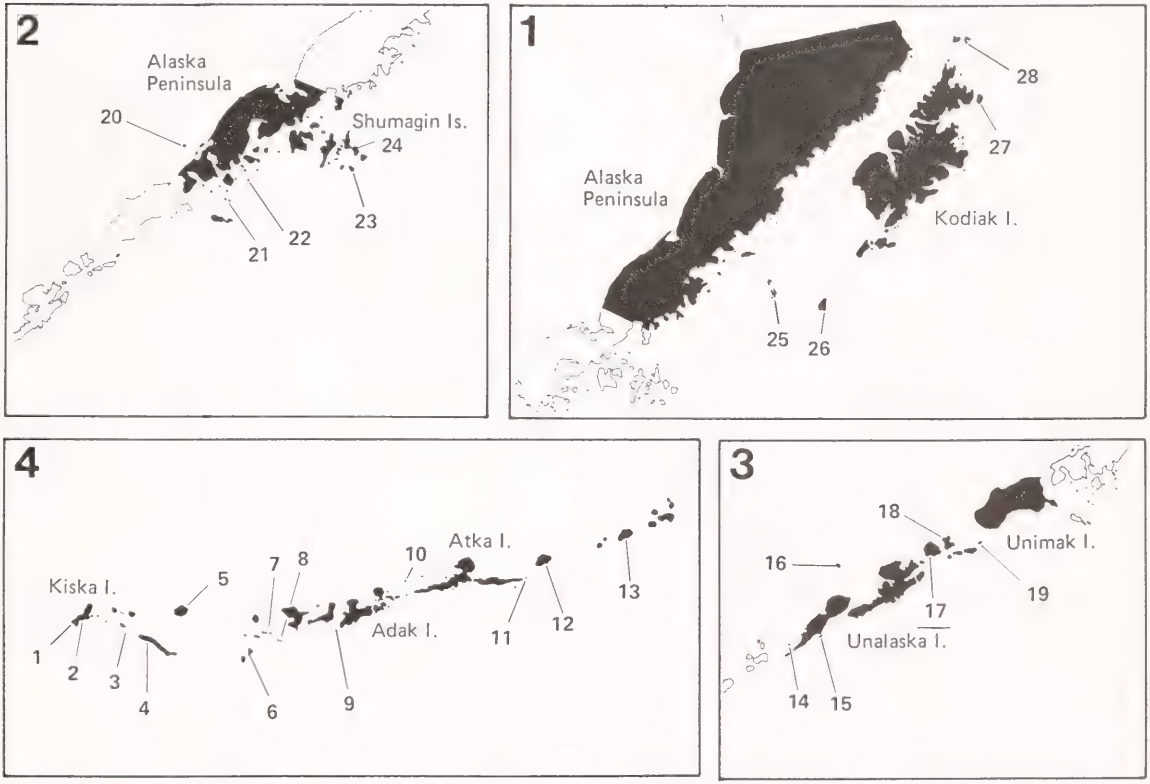
A shipboard survey also was conducted of rookeries and major haul-outs from Ugamak Island to Kiska Island between 25 June and 15 July 1985 (Loughlin et al.[7]). Weather permitting, observers landed at each site and counted the number of northern sea lions present and the number of animals entangled in debris. Pups were counted by first walking through rookeries to drive off the adult and juvenile animals, and then returning to count the pups. This survey was timed to occur after most pups had been born, and before they had begun to enter the water (Withrow 1982).

Pups were counted at northern sea lion rookeries in the central and western Gulf of Alaska between 3 July and 9 July 1984 (Calkins[8]) and between 29 June and 10 July 1986. Access was provided by a skiff launched from a larger vessel or by helicopter.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Loughlin, T. R., P. J. Gearin, R. L. DeLong, and R. L. Merrick. 1986. Assessment of net entanglement on northern sea lions in the Aleutian Islands, 25 June-15 July 1985. Processed Rep. 86-02, 50 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[8]Calkins, D. G. 1985. Draft final report. Steller sea lion pup counts in and adjacent to Shelikof Strait. Submit. to North Pac. Fish. Manage. Coun., March 8, 1985, 13 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.



1, 2 Kiska
3 Ayugadak
4 Amchitka
5 Semisopochnoi
6 Ulak
7 Tag
8 Gramp
9 Adak
10 Kasatochi
11 Agligadak
12 Seguam
13 Yunaska
14 Adugak
15 Ogchul
16 Bogoslof
17 Akutan
18 Akun
19 Ugamak
20 Sea Lion Rock
21 Clubbing Rocks
22 Pinnacle Rock
23 Chernabura
24 Atkins
25 Chowiet
26 Chirikof
27 Marmot
28 Sugarloaf

Pups were counted by driving off the adult animals just ahead of the counting team.

Counts of northern sea lions were made daily by observers on Ugamak Island between 1 June and 3 July 1985 and between 16 June and 26 July 1986. Hourly counts were made between the hours of 0700 and 2400 ADT for 6 days in 1986. Animals were counted from the cliffs above the sites, using 7 × 35 binoculars, a 15-60 power spotting scope, and unassisted vision. Counts were made of animals according to five types: adult territorial male, other adult male, adult female, juvenile, and pup (Merrick 1984). Animals in the water were excluded from counts. Freshly dead pups were recorded when seen, with pup mortality estimated as the total number of dead pups divided by the maximal number of pups counted (living and dead).

Data Analysis

The number of northern sea lions counted in the 1984-86 surveys were compared with counts from surveys in 1956-79 conducted by Kenyon and Rice (1961), Kenyon (fn. 3), Mathisen and Lopp (1963), Braham et al. (1980), Fiscus et al. (1981), and Calkins and Pitcher (fn. 5). Differences in survey areas complicated comparisons for the entire region, so comparisons were generally performed by area.

Comparisons also were complicated by the differences in the counting methods used. Some were counts from land (Fiscus and Johnson 1968[9]; Fiscus et al. 1981; Withrow 1986[10]), while others were estimates from ships (Fiscus and Johnson fn. 9; Calkins and Pitcher fn. 5), and counts from aerial photographs (Mathisen and Lopp 1963; Braham et al. 1980; Calkins and Pitcher fn. 5). The most accurate were visual counts from land and from aerial photos (Withrow 1982); these were the methods used in the 1984-85 aerial surveys.

Several assumptions were made in the analysis of these data. The first was that all sites with more than a few animals were surveyed in 1984-85. Second, the dates and times of peak seasonal and daily abundance were considered to have remained constant throughout the 30-yr period. The 1984-85 surveys and those conducted by Braham et al. (1980) were scheduled to coincide with these peaks; whereas, those of Kenyon and Rice (1961) and Kenyon (fn. 3) were conducted in the spring and without regard to time of day. A smaller proportion of animals were probably onshore in the spring than in the summer (Mathisen and Lopp 1963; Braham et al. 1980). Third, the proportion of the population onshore was assumed to have remained unchanged in the 30 years of counting. Finally, double counting was considered to be negligible in all the surveys because large areas were surveyed in a single day.

Counts presented here are indices of population size because they exclude animals at sea and because it is difficult to count at the exact time peak numbers are ashore. There are few data on the proportion of animals that are at sea at the time the peak number is onshore. Consequently, it was necessary to assume that the proportion had not changed over time. Even during the period when maximal numbers of animals were expected onshore there was variation due to weather and tidal affects (Withrow 1982; Merrick 1984), so that it was unlikely that a survey would occur on the day and time of peak numbers. However, because the sites on Ugamak Island were counted daily, the maximal number counted there was a closer approximation than the aerial survey counts of the actual peak number of animals onshore during the breeding season. Thus the Ugamak Island data were used to determine if seasonal and daily variation in northern sea lion hauling patterns had changed and to assess the potential amount of error (due to counting at the wrong time) in the aerial photo counts.

Rates of decline between two points in time were calculated using the formula

$$N_t = N_0 d^t$$

where N_0 = count in base year
N_t = count in future year t
t = number of years between the base year and year t
d = rate of change, with the percent annual change calculated as $(d - 1) \times 100$.

Area counts were regressed as a linear function of time to determine if trends in population sizes existed. Student's t-test was used to assess the significance of the regressions. Wilcoxon's signed rank test was used for between year comparisons of paired site counts within an area (Hollander and Wolfe 1973).

[9]Fiscus, C. H., and A. M. Johnson. 1968. Site for research on the Steller sea lion, June-July 1968. Processed Rep., U.S. Fish Wildl. Serv., Bur. Commer. Fish., Mar. Mammal Biol. Lab., Seattle, 33 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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RESULTS

1984-86 Survey Findings

The 1984 survey of the eastern Aleutian Islands resulted in a count of 9,833 adult and juvenile northern sea lions on 16 sites (Table 1). The six rookery islands surveyed included 7,934 animals (Table 2), 91% of the total count. One rookery, Adugak Island, and several haul-out sites were not surveyed owing to inclement weather.

A total of 10,802 adult and juvenile northern sea lions were seen in the 1985 survey of the eastern Aleutian Islands (Table 1), which was not significantly different from the 9,833 animals counted there in 1984 ($P > 0.05$). A total of 67,617 animals were counted at 105 sites in the entire study region. Most (60%) of the animals were associated with the 27 rookeries surveyed; the largest rookeries were in the central Gulf of Alaska, notably at Marmot Island, and in the Central Aleutian Islands. The rookery on Semisopochnoi Island was not surveyed; eight previously identified haul-out sites were unoccupied.

Observers in the 1985 shipboard survey counted 4,950 pups at six rookeries in the eastern Aleutian Islands and 9,170 pups at nine rookeries in the central Aleutian Islands (Table 3). In the 1984 and 1986 pup surveys of six rookeries in the Gulf of Alaska (Table 3) 16,278 (excluding Clubbing Rocks and Pinnacle) and 12,025 pups were counted, respectively.

TABLE 1.—Counts and percent declines of adult and juvenile northern sea lions at all sites in spring and summer 1956-85 in the Aleutian Islands and Gulf of Alaska.

Year	Region: Central Gulf of Alaska	Western Gulf of Alaska	Eastern Aleutian Islands	Central Aleutian Islands	Reference[1]
1956		[2]24,320			1
1957	35,150				1
1959				28,115	2
1960			[2]52,530		2
1962				31,040	3
1975			21,221		4
1976	30,677	9,480	22,142		4,5
1977			23,922		4
1978		14,917			5
1979				[2]41,677	6
1984			9,833		7
1985	24,389	6,667	10,802	25,759	7
Decline[3]					
Overall	−31%	−73%	−79%	−8%	
Annual	−1.3%	−4.4%	−6.1%	−0.3%	

[1]Reference: 1—Mathisen and Lopp (1963); 2—Kenyon and Rice (1961); 3—Kenyon (text fn. 3); 4—Braham et al. (1980); 5—Calkins and Pitcher (text fn. 5); 6—Fiscus et al. (1981); 7—this study.
[2]Significant difference ($P < 0.05$) from 1985 using Wilcoxon signed rank test.
[3]Declines calculated from earliest survey date.

Trends in Regional Numbers

Comparison of the 1984-85 aerial surveys with historical data (Table 1) shows that significant ($P < 0.05$) declines have occurred in northern sea lion numbers in the western Gulf of Alaska (−73%), and eastern Aleutian Islands (−79%). The central Gulf of Alaska (−31%) and central Aleutian Island populations may have also declined since 1957-59, though the decreases (−31% and −8%, respectively) were not statistically significant ($P > 0.05$). Note that the central Aleutian Islands numbers increased 34% between 1959 and 1979. This suggests that either the population increased markedly, was supplemented by immigration from other areas (e.g., the eastern Aleutian Islands), or was an artifact of the 1979 survey methodology (i.e., a shipboard survey). Linear regression models (Fig. 2) fitted to these counts indicate that the trends of all areas, other than the central Aleutian Islands, exhibit significant negative slopes ($P < 0.05$).

The number of adult breeding animals has declined in all areas since 1957 except the central Aleutian Islands (Table 2). Numbers at the central Aleutian Islands rookeries increased by 88% between 1959 and 1985, a significant increase ($P < 0.01$). As the overall population in the central Aleutian Islands decreased between 1959 and 1985, this may indicate that a larger proportion of the population is now breeding than in the past. Rookery populations in the eastern Aleutian Islands have declined 79% since 1957, a significant decline ($P < 0.05$). A loss of 15,000 animals occurred at the Ugamak and Akutan Island rookeries alone between 1968 and 1975. Numbers at rookeries in the western and central Gulf of Alaska decreased 66% and 47%, respectively, between 1956-57 and 1985.

Trends in Regional Pup Production

Pup counts are available for only a few sites prior to 1984. These data (Table 3) show that the number of northern sea lion pups counted in the central Gulf of Alaska decreased between 1979 and 1986 by 44%, from 18,998 to 10,600. The number of pups has also declined at sites in the western Gulf of Alaska and eastern Aleutian Islands. Pupping decreased 52% at Bogoslof Island between 1968 and 1985, 89% at Walrus Island (in the Pribilof Islands) between 1960

TABLE 2.—Counts of adult and juvenile northern sea lions on individual rookeries for selected surveys from spring and summer 1956 to 1985 in the Aleutian Islands and Gulf of Alaska.

Island[1]	Year					
	1956-59[2]	1960-62[3]	1968[4]	1976-79[5]	1984[6]	1985[6]
Central Aleutians:						
Kiska (1, 2)	1,000	600		7,155		3,066
Ayugadak (3)	600	1,005		1,463		702
Amchitka (4)	600	1,515		1,943		728
Semisopochnoi (5)	2,500	3,700		1,223		nc
Ulak (6)	1,500	550		3,068		2,729
Tag (7)	400	200		1,740		944
Gramp (8)	700	0		2,235		1,290
Adak (9)	0	0		972		964
Kasatochi (10)	200	2,000		2,166		1,170
Agligadak (11)	250	3,000		993		514
Seguam (12)	25	1,275		6,493		2,942
Yunaska (13)	800	110		2,249		1,071
Total	[7]8,575	13,955		[7]31,700		16,120
Eastern Aleutians:						
Adugak (14)	1,275	1,000	nc[8]	1,177	nc	955
Ogchul (15)	2,966	2,000	nc	1,109	712	547
Bogoslof (16)	2,136	1,100	3,310	3,308	1,379	1,287
Akutan (17)	9,275	15,720	10,316	4,019	2,533	1,710
Akun (18)	nc	2,000	1,900	1,050	760	435
Ugamak (19)	14,536	13,400	13,553	4,760	1,252	1,429
Sea Lion Rock (20)	2,871	2,000	nc	2,076	1,298	538
Total	33,059	[7]37,220	29,079	[7]17,499	7,934	6,901
Western Gulf:						
Clubbing Rocks (21)	1,556			2,663		1,251
Pinnacle Rock (22)	3,142			3,692		1,588
Chernabura (23)	4,806			2,758		487
Atkins (24)	4,995			3,943		1,562
Total	14,499			13,056		4,888
Central Gulf:						
Chowiet (25)	6,014			4,441		2,059
Chirikof (26)	1,695			5,199		2,346
Marmot (27)	3,866			6,381		4,983
Sugarloaf (28)	11,963			4,374		2,991
Total	23,538			20,395		12,379

[1]Rookery island name and code (within parentheses) as in Figure 1.
[2]Mathisen and Lopp (1963).
[3]Kenyon (text fn. 3), for central Aleutian Islands in 1962; Kenyon and Rice (1961), for eastern Aleutian Islands in 1960.
[4]Fiscus and Johnson (text fn. 9).
[5]Fiscus et al. (1981), for central Aleutian Islands in 1979; Braham et al. (1980), for eastern Aleutian Islands in 1976; Calkins and Pitcher (text fn. 5), for western Gulf of Alaska in 1978 and central Gulf of Alaska in 1979.
[6]This study.
[7]Significant difference from 1985 at $P < 0.05$.
[8]nc = not counted.

and 1984, and 76% at Akutan Island between 1965 and 1985 (NMML[11]).

Ugamak Island Surveys

The estimated number of sea lions on Ugamak Island was 14,536 in 1957 and 13,553 in 1968 (Table 2). Significant changes were not observed until 1975-78 (Braham et al. 1980), by which time numbers had fallen to about 4,760 animals. Aerial surveys in 1984 and 1985 found 1,252 and 1,429 animals, respectively.

Ground counts of sea lions on Ugamak Island at comparable sites and survey dates (Table 4) showed a decline of 84% from 10,295 in 1969 to 1,684 in 1986. The decline was greatest between 1969 and 1977 when the count fell by 65%, from 10,295 to 3,577. Numbers fell 53% from 1977 to 1986, and 17% between 1985 and 1986.

The number of breeding animals at Ugamak

[11]Data available from NMML files. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 3.—Counts of northern sea lion pups at sites in the Aleutian Islands and Gulf of Alaska, 1978-86.

Island	Year 1978[1]	1979[1]	1984[1]	1985[2]	1986[2]
Central Aleutian:					
Kiska				882+	
Ayugadak				329	
Amchitka				nc	
Semisopochnoi				nc	
Ulak				1,236	
Tag				703	
Gramp				909	
Adak				558	
Kasatochi				892	
Agligadak				nc	
Seguam		2,475		2,635	
Yunaska				1,026	
Total		2,475		9,170+	
Eastern Aleutian:					
Adugak				844	
Ogchul				172	
Bogoslof		914		1,109	
Akutan				1,130	
Akun				60	
Ugamak				1,635	1,386
Sea Lion Rock				nc	
Total		914		4,950	1,386
Western Gulf:					
Clubbing Rocks	725	1,419	1,394		
Pinnacle	615	2,013	2,748		
Chernabura	545	646	200		379
Atkins	2,750	4,538	2,093		1,046
Total	4,635	8,616	6,435		1,425
Central Gulf:					
Chowiet	4,670	5,485	3,207		1,731
Chirikof	1,573	1,649	1,913		1,476
Marmot	6,140	6,741	5,751		4,286
Sugarloaf	5,021	5,123	3,114		3,107
Total	17,404	18,998	13,985		10,600

[1]Calkins and Pitcher (text fn. 5), except for Seguam and Bogoslof Islands, which are from Fiscus et al. (1981).
[2]This study and Loughlin et al. (text fn. 7).

TABLE 4.—Counts of adult and juvenile northern sea lions at Ugamak Island, AK, mid-June 1969-86[1].

Rookery or haul	1969[2] Date	1969[2] Count	1977[3] Date	1977[3] Count	1985[4] Date	1985[4] Count	1986[4] Date	1986[4] Count
South								
Cone	6/20	400+	6/28	337	6/20	68	6/20	59
Eagle	6/18	1,000+	6/28	412	6/20	95	6/20	85
Ugamak Bay								
A1	6/19	639	6/20	148	6/20	139	6/20	133
A2	6/19	1,583	6/20	406	6/20	439	6/20	546
A3	6/19	257	6/20	27	6/20	3	6/20	35
A4	6/19	1,467	6/20	369	6/20	272	6/20	15
A5	6/12	720	6/28	364	6/20	361	6/20	336
Total south		6,066		2,063		1,377		1,209
North								
North Point								
N1	6/19	576	6/19	80	6/20	1	6/20	0
N2	6/19	262	6/19	56	6/20	9	6/20	15
N3	6/19	197	6/19	330	6/20	3	6/20	2
NE Point								
NE1	6/14	975	6/19	429	6/20	328	6/20	156
NE2	6/14	1,400	6/28	500	6/20	315	6/20	302
North haul	6/19	819	6/28	119	6/20	0	6/20	0
Total north		4,229		1,514		656		475
Grand total		10,295		3,577		2,033		1,684

[1]Excludes three sites not counted in all four years. Last day of counting in 1969 was 20 June, so this table is designed to provide comparable data from other years only, and will not match the maximal count for the year. Sites are identified using scheme developed by Fiscus (text fn. 12).
[2]From Fiscus (text fn. 12).
[3]From land counts, except counts from 28 June 1977, which were taken from aerial photographs (Withrow (text fn. 10)).
[4]This study.

Island has not declined equally at all sites (Table 4). Numbers on the south side of the island at Ugamak Bay declined until 1977, and then changed very little through 1985. However, in 1986 one south side site (A4) was abandoned by breeding females, whereas it had been occupied by over 400 in the previous year. Numbers at north side sites have declined through the present, with most sites there now

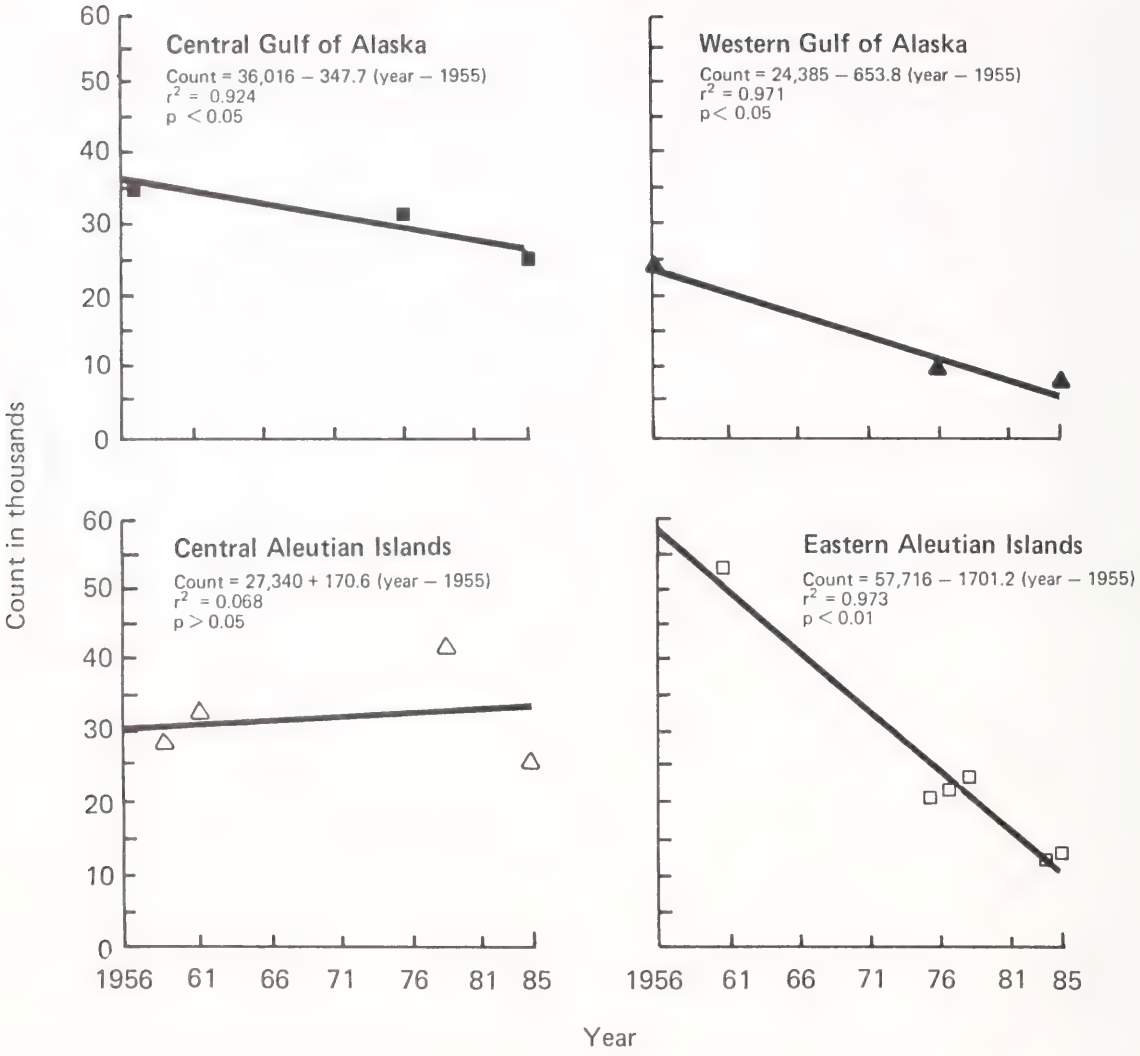

FIGURE 2.—Trends in total adult and juvenile northern sea lion abundance by area in Alaska, for spring and summer surveys conducted from 1956 to 1985.

empty. Although some rookeries have been reduced in size and decreases have been observed in all age and sex groups, the ratio of adult females to territorial males has remained relatively constant between 1977-78 (14.4-17.3) and 1986 (16.4). Between 1985 and 1986, however, the number of adult males remained constant, while the number of females decreased by 26%.

Island totals of juveniles were similar in 1985 (87 animals) and in 1986 (110 animals). However, an analysis of comparable areas of the island (i.e., N1-N3 and A2-A4; Fiscus[12]) indicated that the juvenile portion of the population had decreased significantly ($\chi^2 = 4.09$, $P < 0.05$) from 9.0% in 1977 to 1.4-1.6% in 1985-86. A comparably low rate (2%) has only been observed at Año Nuevo Island (Gentry 1970) and that rate was calculated for a single primary rookery rather than a whole island. Rates such as the 22% observed at Marmot Island in 1983 or the 25% observed for British Columbia in 1956 seem more typical for northern sea lion rookeries (Pike and Maxwell 1958; Merrick 1984).

Counts of pups were available for six rookeries

[12]Fiscus, C. H. 1970. Steller sea lions at Ugamak Island, Aleutian Islands, Alaska, June 1969. Unpubl. Rep., U.S. Fish Wildl. Serv., Bur. Commer. Fish., Mar. Mammal Biol. Lab., Seattle, 78 p. Northwest and Alaska Fish. Cent. Natl. Mar. Mammal Lab., NMFS, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

on the island for 1969, 1977, 1985, and 1986 (Fiscus fn. 12; Withrow fn. 10). The number of pups declined by 72% between 1969 and 1977, with two rookeries abandoned. A decline of 35% occurred between 1977 and 1986, with three more rookeries abandoned. Pupping has probably declined on other parts of the island, because the number of breeding animals decreased at other rookeries (Table 4) where pups were not counted in 1968 and 1977. Between 1985 and 1986, the only years with complete island surveys, there was a decline of 18% in pup numbers. Despite the decline in the number of pups born, the ratio of pups to adult females has increased from 0.75 in 1968 and 0.73-0.81 in 1977-78 to 0.95-1.06 in 1985-86. The Ugamak Island pup mortality during the first 1-2 mo postpartum in 1985-86 was 3.4-4.5%. Median pupping dates were similar in 1977-78 (13 June) and 1985 (12 June).

Finally, the Ugamak Island data allowed an evaluation of the times of peak abundance and variability in the counting methods. Counts peaked in 1985-86 between the third week of June and the first week of July, with 90% of the maximal breeding season population onshore at midday during this period. Hourly counts between 1000 and 2000 ADT during this period were always within 10% of the day's maximum. These occupancy patterns were the same as those observed by Withrow (1982) at Ugamak Island in 1977-78.

The Ugamak Island data also were used to provide an estimate of the accuracy of the 10 June 1985 aerial survey of the island. There was only a 3% difference between the aerial photo count and the simultaneous ground count. Thus, as noted by Withrow (1982), aerial photo counts accurately reflect ground counts. Despite this accuracy, the aerial photo count of 10 June 1985 was 24% lower than the maximal ground count of 25 June 1985. This bias was likely caused by the aerial survey occurring slightly before the period of peak abundance.

DISCUSSION

The number of northern sea lions found at sites within the study region, which included at least 140,000 animals circa 1958, totaled less than 68,000 in 1985—a decline of 52% (−2.7% per year). All indicators (regional numbers, breeding animals on rookeries, pup production, and the Ugamak Island data) confirm this decline. The rates of decline are probably underestimated because declines probably did not begin until after 1958. For example, the Ugamak Island population showed no decline between 1957 and 1969, and then declined at least 10.1% per year between 1969 and 1986. This indicates that the eastern Aleutian Island northern sea lion population may have begun to decline in the early 1970s rather than in 1958, the base year for rate calculations. Data are insufficient to calculate regional or area rates from 1969 to later dates.

Declines may have occurred in two phases. The first phase may have begun in the 1970s and been confined to the eastern Aleutian Islands and western Gulf of Alaska. Numbers for the entire study region fell by 25% (−1.6% per year) between 1958 and 1977. Numbers in the eastern Aleutian Islands appeared to stabilize in the mid-1970s, while those in the central Aleutian Islands and western Gulf of Alaska may have increased. A second phase of the decline may have begun during the late 1970s, with all areas being affected and overall numbers falling 36% (−5.2% per year) between 1977 and 1985. Results of the 1986 pup survey and 1986 Ugamak Island study indicate that the decline is still continuing.

Alternative Explanations for the Declines in Northern Sea Lion Numbers

Consideration has been given as to whether the declines could be explained by counting errors or biases, changes in northern sea lion behavior, or emigration. However, errors in counting or, for that matter, changes in technique do not explain the decline in numbers. Because counts taken in the 1950s and 1960s were conducted in the spring (before abundance had peaked on land) and because sites were missed, we believe that they underestimated sea lion numbers. Braham et al. (1980) estimated that only 42% of the eastern Aleutian Island sites were surveyed in 1957 (Mathisen and Lopp 1963). Animals present were probably accurately counted in the pre-1970 surveys because observers were all experienced. Kenyon and Rice (1961) compared their visual counts to concurrent aerial photos taken and found that their error was between 6 and 10%. Even if they had overestimated numbers the error may have been counterbalanced by any underestimate from counting too early in the year. The counts of the 1970s and 1980s were probably more comparable because they were made during the period of peak numbers onshore. Also there was little variation during this period in methods and personnel were experienced in these survey techniques. Furthermore, the methods used were believed to have been the most accurate. Even if all of the aerial counts were lower than the maximal

count for the season (as observed at Ugamak Island in 1985), the amount of error would be insufficient to explain the low counts. In any event, the declines in northern sea lion numbers observed in aerial surveys since the 1970s have been confirmed by the counts made from land at Ugamak Island and by the pup counts taken in the eastern Aleutian Islands and the Gulf of Alaska.

Pup counts can provide a reliable index of population change since almost all pups born can be counted in surveys scheduled prior to the pups going to sea. However, the index may be biased (Berkson and DeMaster 1985). Briefly stated, if precount pup survival (e.g., live birth rates) is density-dependent the counts would overestimate the rate of decline. If postcount pup survival (e.g., juvenile survival) is density-dependent then the counts would underestimate the rate of decline. Finally, if adult survival is density-dependent there would be little bias. Few data exist on density-dependent population regulation in northern sea lions, so we cannot be sure which, if any, of these mechanisms are operative. However, available data suggest that while precount survival in recent years is either unchanged or has improved, postcount survival has decreased. In both cases, the effect would be for pup counts to understate the rate of decline.

It is unclear whether northern sea lion hauling behavior has changed sufficiently to affect the counts. The 1977-78 and 1985-86 Ugamak Island data show that seasonal and daily hauling patterns and the timing of critical events (e.g., the median pupping date) have not changed. Similar data are not available for the earlier surveys. Animals may have dispersed to other sites, but they still would have been counted in the regional surveys. There is some evidence from Ugamak Island that females may spend less time ashore now than before (e.g., the high ratio of pups to adult females), which would decrease the number of adult animals counted. The low number of juveniles counted at Ugamak Island in 1985-86 may simply reflect increased juvenile dispersal away from the site due to changing prey resources and earlier weaning.

The decline in northern sea lion numbers onshore in the region has not been due to the emigration of animals to other regions because significant increases have not been noted elsewhere. Numerical decreases have been noted at the western extent of the breeding range in the Kuril and Commander Islands (Perlov 1982; Kuzin et al. 1984; Chelnokov 1984). Numbers began to fall in this region circa 1972, and by 1981-82 had fallen by 50% or more. Abundance at sites in the western Aleutian Islands declined 34-61% from 1979 to 1985 (Klett[13]). Adult northern sea lions at the Pribilof Islands have declined in number from approximately 7,000 animals in 1960 to 1,100 in 1981 (Kenyon 1962; Loughlin et al. 1984). Most of these animals were located at Walrus Island which was occupied by 4,000-5,000 northern sea lions in 1960, around 1,500 in 1975, and only 600 in 1982 (Kenyon 1962; NMML fn. 11). In 1960, 2,866 pups were counted at Walrus Island, but this number had fallen to 334 by 1982 (Kenyon 1962; NMML fn. 11). Northern sea lions are regularly seen farther north at St. Matthew and St. Lawrence Islands during the ice-free season, but the total has rarely exceeded 300 animals (Loughlin et al. 1984). Frost et al.[14] estimated 2,000 animals were in northern Bristol Bay during the 1970s, with 1,500 observed in the summers of 1980-82. The only rookery in Bristol Bay, Sea Lion Rock (Table 1), has decreased in size by 81% since the counts of 1957 reported by Mathisen and Lopp (1963). The 1982 count of 7,962 animals in southeast Alaska was not substantially different from the 1973 estimate of 8,430 (Calkins and Pitcher[15]). The number of northern sea lions in British Columbia and in the lower United States (i.e., Washington, Oregon, and California) do not appear to be increasing from 5,700 and 5,410 animals, respectively (Loughlin et al. 1984; Bigg 1985).

Proximate Causes of the Decline

The declines of northern sea lion could either be due to falling reproductive rates or reduced survival of pups, juveniles, and adults (especially females). There does not, however, appear to have been significant declines in reproductive rates or in pup survival 1-2 mo postpartum. The pregnancy rate of females taken in the Gulf of Alaska during April-May 1985 was 62% (n = 62), which was not significantly different from the 67% (n = 102) found there in 1975-78 (χ^2 = 0.002, $P > 0.50$; Pitcher and Calkins 1981; Goodwin and Calkins[16]). In addition,

[13]E. Klett, U.S. Fish and Wildlife Service, Aleutian Island Unit, Alaska Maritime National Wildlife Refuge, Box 5251 Naval Air Station, Adak, AK 98791, pers. comm. March 1986.

[14]Frost, K. J., L. F. Lowry, and J. J. Burns. 1982. Distribution of marine mammals in the coastal zone of the Bering Sea during summer and autumn. Alaska Dep. Fish Game, Final Rep. RU613, 188 p. Alaska Department of Fish and Game, 1400 College Road, Fairbanks, AK 99701.

[15]Calkins, D. G., and K. Pitcher. 1983. 1982 pinniped investigations in southern Alaska. Unpubl. rep., 15 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[16]Goodwin, E. A., and D. G. Calkins. 1985. Preliminary results of ongoing investigations of San Miguel Sea Lion Virus, Leptospirosis, and Chlamydiosis in Alaska Steller sea lions and their rela-

the ratio of pups to adult females at Ugamak Island has increased since 1968 and 1977-78. The 3.4-4.5% rate of pup mortality at Ugamak Island was low when compared with the 11% found at Marmot Island, 10% at Año Nuevo Island, CA, and the 13-14% at Wooded Island, AK (Gentry 1970; Sandegren 1970; Merrick 1984).

The declines of northern sea lion may be due to reduced survival of pups (after they go to sea), juveniles, and adults. Changes in survival rates are difficult to assess. The precipitous declines in pupping in the Gulf of Alaska (Table 3) may indicate that there have been large declines in the female population there. Numbers of adult females at Ugamak Island also declined between 1985 and 1986. The Ugamak Island data also seem to indicate that juvenile abundance was much lower in 1985-86 than at other sites and in other years, which may indicate unusually high mortality is occurring after pups leave the rookery. Investigation of the declines in juveniles and adult females may hold the greatest promise for further study.

Ultimate Causes of the Decline

The causes of the reduced fecundity or survival of northern sea lions are presently unknown, but there are several possibilities—disease, changes in prey resources, and the combined effects of these and other factors. Disease and prey limitations are particularly plausible causes of the decline because of their potential for widespread impacts (hence declines in other regions) and because they could be implicated in the apparent declines of other Bering Sea and North Pacific Ocean pinniped populations. The number of northern fur seals, *Callorhinus ursinus*, breeding at the Pribilof Islands and on Robben Island in the Sea of Okhotsk have decreased since the mid- to late 1970s (Fowler 1985). Since the 1970s, harbor seal, *Phoca vitulina richardsi*, numbers may have decreased in Bristol Bay (Pitcher[17]) and have declined substantially in the central Gulf of Alaska at Tugidak Island (Calkins and Pitcher[18]).

Diseases resulting in reproductive failures and neonate, juvenile, and adult mortality could be a significant source of mortality. Antibodies to two types of bacteria (*Leptospira* and *Chlamydia*) and one marine calicivirus virus (San Miguel Sea Lion Virus) which could produce such mortality were present in blood taken from northern sea lions in Alaska (Fay et al. 1978[19]; Goodwin and Calkins fn. 16; Barlough et al. in press). Leptospires are spirochete bacteria and are suspected agents of abortion and adult mortality in California sea lions, *Zalophus californianus*, (Smith et al. 1974a) and in northern fur seals (Smith et al. 1974b). San Miguel Sea Lion Virus may also be associated with reproductive failures or neonatal deaths in California sea lions and northern fur seals, although the evidence is limited (Smith et al. 1973). *Chlamydia* has not been studied previously in sea lions. These and other agents are being examined for their possible adverse effects on northern sea lion populations.

The decline in northern sea lion numbers may be related to changes in the quantity and size of their prey. The few studies of the food habits of northern sea lions indicated that their primary prey are walleye pollock, *Theragra chalcogramma*, in the Bering Sea, Gulf of Alaska, and North Pacific Ocean (Klumov 1957; Pitcher 1981; Calkins et al.[20]). This fish is also a major prey item of harbor seals and northern fur seals (Pitcher 1980; Kajimura 1984). Walleye pollock biomass in the eastern Bering Sea rose from less than 5 million metric tons (t) in the 1960s to a peak of over 13 million t in the early 1970s and has since declined to about 8 million t in 1985 (Bakkala et al. in press). While the population biomass remains high, sporadically low abundance of age-1 walleye pollock between 1979 and 1984 could mean that in some years (e.g., 1981, 1982, and 1984) there would be fewer fish in the 10-35 cm range (Bakkala et al. in press). This size range includes the mean sizes consumed by northern sea lions and harbor seals (Pitcher 1981; Frost and Lowry 1986). Declines in abundance and increases in fish length have also been noted since 1981 in the Shelikof Strait region of the Gulf of Alaska (Nelson and Nunnallee 1985). However, there are few data on northern sea lion foraging patterns in the Bering Sea and

tionship to declining pup counts. Presented at the Sixth Biennual Conference on Biology of Marine Mammals, Vancouver, B.C., Nov. 1985. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[17]K. Pitcher, Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502, pers. comm. February 1986.

[18]Calkins, D. G., and K. Pitcher. 1985. Pinniped investigations in southern Alaska: 1983-84. Unpubl. rep., 19 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

[19]Fay, F. H., R. A. Dieterich, L. M. Shults, and B. P. Kelley. 1978. Morbidity and mortality in marine mammals. U.S. Dep. Commer. and U.S. Dep. Inter. (OCSEAP), Environ. Assess. Alaska Cont. Shelf, Ann. Rep., Mar. 1978, 1:39-79.

[20]Calkins, D. G., G. A. Antonelis, Jr., and G. W. Oliver. 1981. Preliminary report of the Steller sea lion/ice seal research cruise of the *ZRS Zvyagino*. Unpubl. rep., 22 p. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99502.

Gulf of Alaska, so a relationship between the declines in northern sea lion numbers and changes in the abundance of their prey cannot be rejected or confirmed.

The declines of northern sea lion may not have a single cause, but may be due to the effects of a combination of these and other factors. Sources of mortality which alone seem insufficient to account for the declines but which could be important in a combined effect include the pre-1973 commercial sea lion harvests, entanglement in marine debris, incidental taking in fisheries, and the killing of sea lions for bait and predator control.

Northern sea lions were commercially harvested in the eastern Aleutian Islands and Gulf of Alaska from 1959 to 1972. Six hundred and sixteen adult males were taken in an experimental harvest in 1959 (Thorsteinson et al. 1961). A total of 45,178 northern sea lion pups of both sexes were harvested in the eastern Aleutian Islands and Gulf of Alaska between 1963 and 1972 (FEIS[21]). The largest harvests were conducted between 1963 and 1972 at Sugarloaf and Marmot Islands where 16,763 and 14,180 pups, respectively, were killed, and between 1970 and 1972 at Ugamak and Akutan Islands where 3,773 and 6,036 pups, respectively, were killed. The pup harvests, which sometimes reached 50% of the total pup production from a rookery (e.g., at Sugarloaf Island in 1965 and 1968), could have depressed recruitment in the short term. This may partially explain the declines experienced at some sites through the mid-1970s. However, it is unclear why numbers declined in areas where no harvest occurred (e.g., the north side of Ugamak Island), while no declines were observed at some harvest sites (e.g., Marmot Island). In any event, those harvests should not currently be affecting the decline, because populations should have stabilized 3-5 years after the cessation of harvesting as unharvested year classes reached breeding age. Furthermore, these harvests probably cannot explain the declines in numbers counted in the western and central Aleutian Island populations.

Little information exists on the effect of entanglement in marine debris on northern sea lions. Despite debris commonly being found in areas northern sea lions frequent (Calkins 1985; Merrell 1985), data from NMML surveys suggest that this is not a problem, at least for adult sea lions. Observed entanglement rates were 0.07% in the 1985 ship survey (Loughlin et al. fn. 7), 0.09-0.17% in the 1985-86 Ugamak Island surveys, and 0.12% at Marmot Island in 1983 (Merrick 1984). Numerous northern sea lion pups were seen in the November 1985 eastern Aleutian Island entanglement survey (Loughlin et al. fn. 7), but none were entangled. Nevertheless, it is possible that entangled northern sea lion pups drown and are not observed.

Numerous northern sea lions have been taken incidental to fisheries in the Bering Sea and Northeast Pacific Ocean since the late 1960s and early 1970s (FEIS fn. 21). In 1978-81 the estimated average annual mortality for all foreign vessels was 724 animals (Loughlin et al. 1983). This does not, however, include animals taken by U.S. fishermen fishing in joint ventures or independently. Loughlin and Nelson (1986) documented the take in the Shelikof Strait joint venture walleye pollock fishery where an estimated 958 to 1,436 northern sea lions were caught by U.S. trawlers in 1982. This take declined to less than 400 animals per season in 1983 and 1984, probably due to changes in fishing technique and the area and times fished. The cumulative impact of foreign independent and joint venture fisheries in the Bering Sea and North Pacific Ocean probably now accounts for less than 500 deaths per year (NMML fn. 11). Domestic fishermen now working independently probably take less since they generally are involved in fisheries that catch few sea lions. However, as foreign fishing is phased out of U.S. waters, the domestic take will probably increase. The foreign and domestic incidental take contributes to but cannot totally account for the decline.

We are uncertain how the killing of northern sea lions by fishermen has affected the population. Fishermen have been observed to kill adult animals at rookeries, haul-outs, and in the water near boats, but the magnitude of this take is generally unknown. Trawl fisheries attract many northern sea lions during haulback operations and shooting at these animals is a common occurrence. One of the few estimates of shooting mortality comes from Matkin and Fay[22] who calculated that 305 northern sea lions were killed directly (shot) while interferring with fishing operations in the spring 1978 Copper River Delta salmon gill net fishery. Northern sea lions at

[21]Final environmental impact statement (FEIS). 1977. Consideration of a waiver of the moratorium and return of management of certain marine mammals to the State of Alaska. Vol. II. U.S. Dep. Commer. and U.S. Dep. Inter., Interagency Task Group, Wash., D.C., 251 p.

[22]Matkin, C. O., and F. H. Fay. 1980. Marine mammal-fishery interactions on the Copper River and in Prince William Sound, Alaska, 1978. Final rep. for contract MMC-78/07 to Mar. Mammal Comm., 71 p. Available from National Technical Information Service, U.S. Department of Commerce, Springfield, VA 22161, as PB80-159536.

sites in the eastern Aleutian Islands also would have been prime sources of bait for crab fishermen. Thus it may be more than a coincidence that the onset of the northern sea lion decline in the eastern Aleutian Islands began at the time of peak landings in the Bering Sea king crab (*Paralithodes* spp., *Lithodes aequispina*) and Tanner (snow) crab (*Chionoecetes* spp.) fisheries. Killing "nuisance" northern sea lions continues to this date (R. L. Merrick pers. obs.). This killing may have a significant effect on local populations (e.g., the eastern Aleutian Islands and central Gulf of Alaska) and might have caused animals to disperse away from traditional rookeries and haul-outs. It should have little effect, however, in areas that have not been heavily fished (e.g., the western and central Aleutian Islands).

Sources of mortality that we think are of minor or unknown importance in the decline include changes in oceanographic or climatic conditions, increased predation, harassment, subsistence harvests, and chemical pollutants.

Prospects for the Future

Many pinniped species have experienced population declines within recent history, and in most cases the population has been able to rebuild. Overexploitation has been a cause of long-term but temporary declines in many species, including Southern Hemisphere fur seals (*Arctocephalus* spp.), elephant seals (*Mirounga* spp.), and northern fur seals (Bonner 1982). Other human activities have caused declines, such as that of ringed seals, *Phoca hispida*, in the Baltic Sea, where organochlorines may have caused a high rate of reproductive failures (Helle et al. 1976). Natural mortality and temporary local declines have resulted from influenza outbreaks in northwest Atlantic Ocean harbor seals, *Phoca vitulina concolor*, (Geraci et al. 1983), and Leptospirosis epizootics in California sea lions (Vedros et al. 1971). Decreased prey abundance may have reduced the ringed seal and bearded seal, *Erignathus barbatus*, populations in the eastern Beaufort Sea in 1974-75 (Stirling et al. 1982).

Thus the northern sea lion decline in southwestern Alaska is not unique among pinnipeds, but the causative factor remains difficult to identify. Based on these other examples we can estimate what the ultimate effect of the most plausible hypotheses will be on the population. If one of the causes of the decline is disease, then the population will stabilize and begin to increase once the epizootic has run its course. If a change in prey quantity or quality has reduced the carrying capacity of the Bering Sea, Gulf of Alaska, and North Pacific Ocean for northern sea lions, then the population should stabilize if the critical resource stabilizes. If the decline is caused by a combination of factors, then the outcome cannot be determined. Though serious, the current reduced status of the stock in southwestern Alaska does not yet imperil the population, because a large reservoir of adult breeding animals remains to rebuild the population should the decline abate.

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ON THE ESTIMATION OF NUMBERS OF NORTHERN FUR SEAL, *CALLORHINUS URSINUS*, PUPS BORN ON ST. PAUL ISLAND, 1980-86

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ABSTRACT

Since 1962, the numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island have been determined using a mark-recapture procedure. We investigate the feasibility of determining estimates of the total pup population on the 14 rookeries of St. Paul Island from subsamples of rookeries. Estimates are derived from simple random sampling and stratified (by rookery size) random sampling using standard ("blow up") estimation procedure, and ratio and regression estimates (based on the same sampling procedure but taking advantage of a strong relationship between numbers of breeding males and live pups on the various rookeries). Evaluation of the sampling schemes and estimation methods is based on the performance of the estimators for 3 years (1965, 1970, 1975) of data for which the mark-recapture estimates from all 14 rookeries were available. Ratio estimates are preferred to estimates obtained from the standard procedure for both simple random sampling and stratified random sampling. Furthermore, estimates from sampling plans based on three strata proved more satisfactory than those based on either unstratified or two-strata sampling. The ratio methods are applied to data collected during 1980-86. The number of northern fur seal pups born on St. Paul Island decreased at approximately 7.5% per year during 1975-81. There was no statistically detectable trend in numbers born during 1981-86.

The number of northern fur seals, *Callorhinus ursinus*, born on St. Paul Island (approximately 80% of the total Pribilof Islands herd production) has been determined in a variety of ways since the United States assumed direct management of the fur seal herd in 1910 (Parker 1946). The history of northern fur seal population estimation during 1912-47 and analyses of the reliability of methods then proposed for estimating numbers of pups are presented in Kenyon et al. (1954). The evolution of the "shearing-sampling" method, a variant of the mark-recapture technique, is discussed in Chapman (1964) and Chapman and Johnson (1968).

Since 1962, the estimate of the size of the pup population has been obtained using the "shearing-sampling" method. The safety of the crew, the accuracy of the estimate, and the minimization of disturbance to rookeries are major concerns; hence, the work is done as the breeding structure breaks up, but before pups spend most of their time in the water. During early August, a large number of pups (approximately 10% of the population) are marked by shearing a small patch of hair from the top of their heads; this exposes the pale underfur and produces an easily identifiable mark. The marking effort is allocated throughout the rookery so that each pup has an approximately equal chance of being marked. A few days later, each rookery is sampled twice during different periods to estimate the proportion of marked animals on the rookery. Thus, estimates of the population size and its variance can be calculated for each rookery. The estimate of the population present at the time of shearing is the number of sheared animals divided by the proportion of sheared pups among all those resighted—the normal Petersen estimate. The variance of this estimate is one-fourth the squared difference of the two estimates.

The purpose of this paper is to demonstrate the feasibility of obtaining accurate estimates of the total pup population on St. Paul Island from "shearing-sampling" estimates on a few sample rookeries. The advantages of obtaining estimates of the population from a subsample of rookeries include 1) less disturbance on the total northern fur seal population (each season that pup production is estimated on a particular rookery, crews must traverse the rookery four times—once to do the marking, twice to estimate the proportion of marked pups among the population, and once to count the number of dead pups); and 2) considerable savings in time, energy, and funds.

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METHODS AND AVAILABLE DATA

The data (Table 1) used for evaluating procedures for estimating the size of the pup population on St. Paul Island were the counts of breeding males made in mid-July and the estimate of the size of the pup population made in early August.

We assumed that for any year, the sum of the estimated numbers of live pups from each of the 14 rookeries, T, was the known or "true" size of the population. Estimates of the variances of each rookery were available; we assumed that the counts from each rookery were independent and estimated the variance of the total population, σ^2, as the sum of the estimated variances on the 14 rookeries. An approximate 95% confidence interval for the total population was $T \pm t(0.975,14)\,\sigma$, where $t(0.975,14)$ is the 97.5 percentile of Student's t distribution with 14 degrees of freedom.

Two sampling schemes and three estimation procedures were investigated. In particular, estimates based on the standard procedure or the "blow-up" estimate, were compared with ratio and regression estimates, which take advantage of a strong correlation between the numbers of breeding bulls and numbers of pups on the rookeries (Figs. 1, 2); these estimation procedures were compared under both simple random sampling and stratified random sampling schemes. For each sampling scheme, all possible subsamples of the 14 rookeries were generated, and the distributions of estimates for each of the 3 years of data were constructed. To determine how well the estimates predict the "true" population, we computed the fraction of (nominal) 95% confidence intervals about the estimate which contained the "true" value (the actual confidence level of the 95% confidence region). In addition, we computed the variance, bias, and the average half-width of the nominal 95% confidence interval of each estimator under the given sampling design.

"Blow-up" estimates of the total numbers of pups on the rookeries under simple random sampling, T_{BU}, were calculated in the following way (Cochran 1977): Let $(P_1, P_2, \ldots P_n)$ be estimates of pup numbers on n sample rookeries. The total on all rookeries was approximated by multiplying the average number of pups on the sample rookeries by the total number of rookeries:

$$T_{BU} = \frac{14}{n} \sum_{i=1}^{n} P_i = 14\,\bar{P}. \qquad (1)$$

The estimate of the variance of this estimate is

$$\mathrm{Var}(T_{BU}) = \frac{14 - n}{n} \frac{14}{n(n-1)} \sum_{i=1}^{n} (P_i - \bar{P})^2 + \frac{14}{n} \sum_{i=1}^{n} \mathrm{Var}(P_i). \qquad (2)$$

When sampling was stratified, the above procedure was applied to each stratum. The total number of pups on all rookeries was estimated as the sum of the estimates on all strata; the variance was approximated by applying Equation (2) to each stratum and then summing over the strata.

Other methods of estimating the total number of pups on all rookeries, when a total count of breeding males was available, were suggested through an examination of the regression equations of numbers

TABLE 1.—Numbers of northern fur seal pups counted and their standard deviations, numbers of breeding bulls, and ratio of pups counted to breeding males for the rookeries of St. Paul Island, AK for 1965, 1970, and 1975.

	1965				1970				1975			
Rookery	Pups	SD	Bulls	Ratio	Pups	SD	Bulls	Ratio	Pups	SD	Bulls	Ratio
Vostochni	34,208.0	2,091.6	1,434	23.9	33,808.5	4,797.7	791	42.7	41,356.0	2,300.9	799	51.8
Tolstoi	25,122.0	294.2	876	28.7	22,194.0	1,759.3	570	38.9	31,107.5	1,375.3	621	50.1
Zapadni	25,066.0	4,228.5	978	25.6	33,665.5	1,112.3	664	50.7	36,815.5	4,413.1	610	60.4
Reef	29,032.5	488.6	1,179	24.6	24,907.0	4,464.7	716	34.8	27,561.0	1,050.8	622	44.3
Morjori	15,434.5	204.4	739	20.9	14,894.0	3,624.6	352	42.3	21,284.5	3,926.6	376	56.6
Polovina Cl.	18,547.5	491.4	650	28.5	17,092.5	1,880.2	390	43.8	24,869.5	4,017.1	461	53.9
L. Zapadni	14,306.0	1,937.5	551	26.0	15,240.0	739.6	325	46.9	21,168.0	2,115.7	363	58.3
Kitovi	11,361.0	244.7	486	23.4	12,713.0	1,678.7	241	52.8	12,965.0	2,511.0	267	48.6
Gorbatch	16,929.0	1,347.7	674	25.1	15,027.5	1,248.0	385	39.0	17,038.5	761.6	387	44.0
Ardiguen	2,680.5	997.7	105	25.5	3,106.5	77.1	108	28.8	2,774.0	297.0	85	32.6
Lukanin	5,290.0	895.2	204	25.9	5,508.5	1,608.7	107	51.5	5,704.0	868.3	112	50.9
Zapadni Reef	5,259.0	58.0	221	23.8	4,191.5	560.7	106	39.5	7,223.0	657.6	139	52.0
Polovina	5,291.0	2,426.8	220	24.1	3,707.5	222.7	87	42.6	4,354.5	1,130.7	88	49.5
L. Polovina	6,117.5	236.9	236	25.9	3,848.0	257.4	103	37.4	3,415.0	43.8	88	38.8
	214,644.5	6,019.9	8,553	25.1	209,904.0	8,479.6	4,945	42.4	257,636.0	8,558.0	5,018	51.3

of pups as a function of numbers of breeding males (Figs. 1, 2). The analyses of variance of these regressions indicated that the quality of the fits was excellent and that the relationship might be used for predictive purposes. No intercepts, except that for 1916 data, were significantly ($P > 0.95$) different from 0. We were interested in subsampling the rookeries (possibly conducting the estimation on as few as four rookeries) and therefore, if a regression estimator were to be used, it was desirable to reduce the number of parameters as much as possible. Inasmuch as the intercepts were not different from 0, the simpler model with no intercept was considered appropriate. Since the variance of the pup estimates was not constant for each rookery, weighting appeared necessary. The variance of the estimates of pup numbers was roughly proportional to the number of bulls, and in such cases (Draper and Smith 1966), the best estimate of the slope of regression line is the average number of pups divided by the average number of bulls (equivalent to the ratio of the total number of pups to the total number of bulls). In this case, the total number of pups on all rookeries was estimated in the following manner: Let $P_1, \ldots, P_n$ and $B_1, \ldots, B_n$ be as above, and B a count of the total number of bulls on all rookeries. Then the total number of pups on all rookeries may be estimated as

$$T_R = \frac{B \sum_{i=1}^{n} P_i}{\sum_{i=1}^{n} B_i} = r\,B. \qquad (3)$$

One estimate of the variance of this ratio estimator is

$$\mathrm{Var}\,(T_R) = \frac{B^2}{\left(\sum_{i=1}^{n} B_i\right)^2} \sum_{i=1}^{n} \mathrm{Var}(P_i) \quad \text{(Cochran 1977).} \qquad (4)$$

When stratified random sampling was used instead of simple random sampling, we calculated the estimator in the same way since the ratio of pups to breeding males did not vary significantly between strata. The difference was due to the evaluation procedures; the number of logical sampling combinations differed and the analysis was restricted to those combinations of sample rookeries that were consistent with the sampling design (e.g., one small rookery, one medium-sized rookery, and two large rookeries).

Another way to estimate the ratio and its variance is with jackknife methods (Mosteller and Tukey 1977). Let r_{-i} be the ratio of pups to breeding males on all but the i^{th} rookery, and r the ratio of pups to breeding males on all the sample rookeries (as in Equation (5)):

$$r_{-1} = \frac{\sum_{i=1}^{n} (n\bar{P} - P_i)}{\sum_{i=1}^{n} (n\bar{B} - B_i)}. \qquad (5)$$

Then, the i^{th} pseudovalue is $r_i^* = nr - (n-1)\,r_{-i}$. The jackknife estimate of the ratio, r^*, is the mean of the r_i^*'s and the variance of r^* is (Mosteller and Tukey 1977):

$$\mathrm{Var}(r^*) = \frac{\sum_{i=1}^{n} (r_i^* - r^*)^2}{n\,(n-1)}.$$

Thus, the jackknife estimate of the total numbers of pups on all rookeries, T_j, is

$$T_j = r^*\,B, \text{ and } \mathrm{Var}(T_j) = B^2\,\mathrm{Var}(r^*).$$

The advantage of the jackknife estimate over the ordinary ratio estimate is the reduction of bias and a simple method of calculating the variance.

The ordinary regression estimate (assuming that the intercept is 0) of the ratio of pups to bulls is

$$s = \frac{\sum_{i=1}^{n} P_i\,B_i}{\sum_{i=1}^{n} (B_i)^2}.$$

Thus, the regression estimator of total numbers of pups is

$$T_{Rg} = sB \text{ and } \mathrm{Var}(T_{Rg}) = B^2\,\mathrm{Var}(s).$$

The estimate of the variance of s is calculated from the mean square residual of the regression equation.

RESULTS

Regressions of numbers of northern fur seal pups

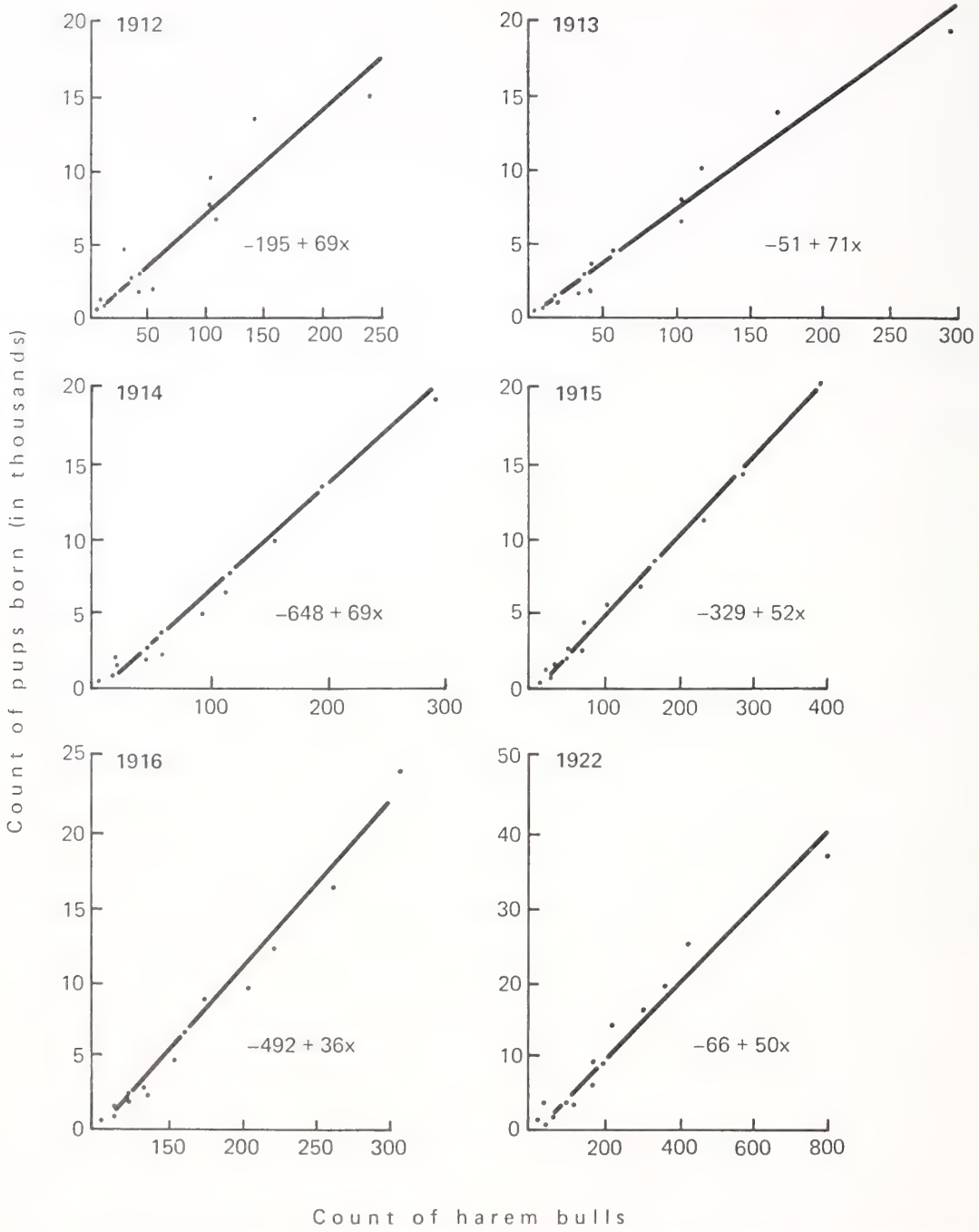

FIGURE 1.—Relationship of counts of northern fur seal pups born to counts of harem bulls for the various rookeries of St. Paul Island, AK, during 1912-22 (data from Lander 1980).

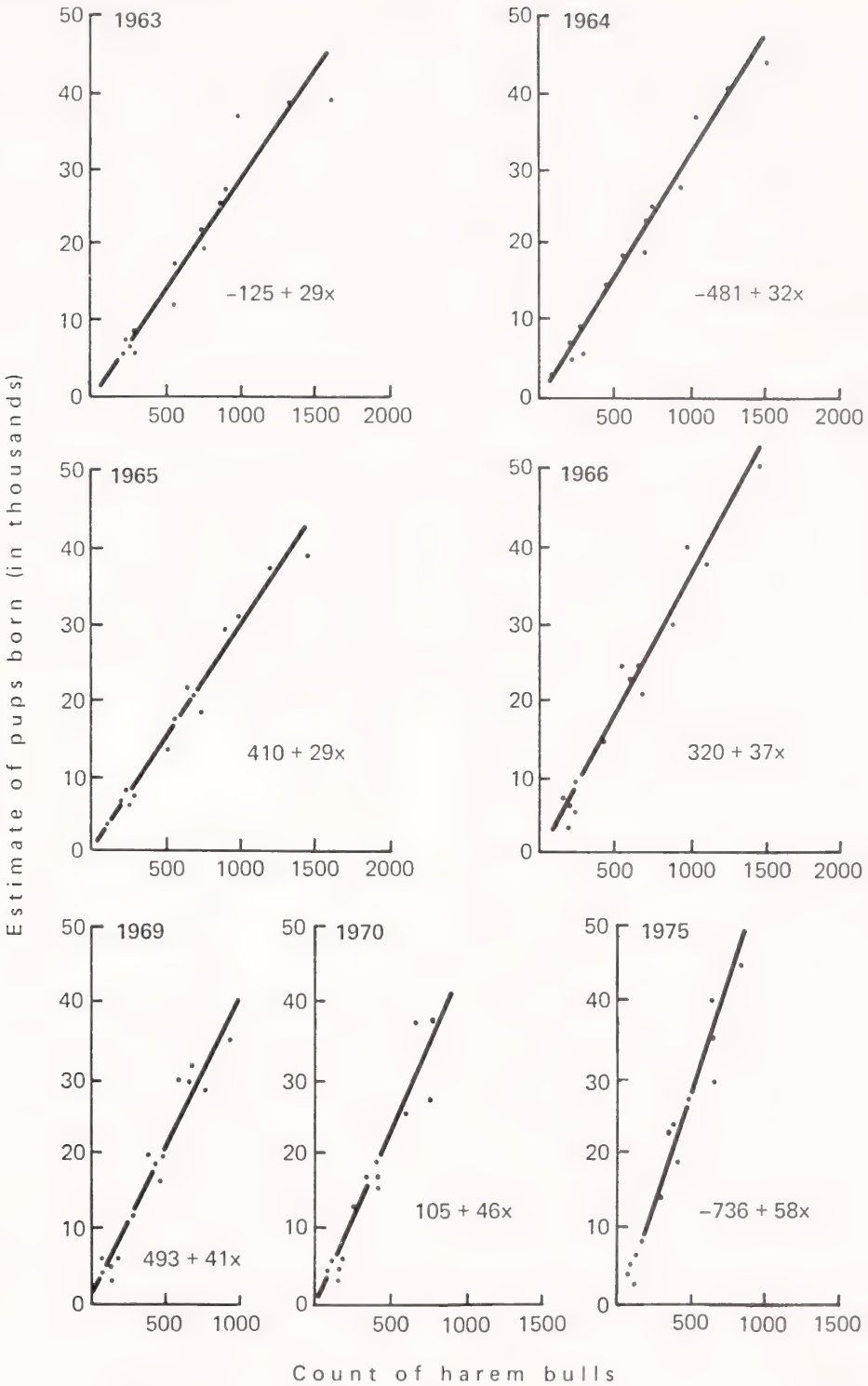

FIGURE 2.—Relationship of estimates of northern fur seal pups born and counts of harem bulls for the various rookeries of St. Paul Island, AK, during 1963-75 (data from Lander 1980).

versus numbers of breeding males for those years in which data were collected on all rookies indicated a strong relationship that could be used for prediction of total pup production if only subsamples of rookeries were censused. The relationship held for those years when censuses of pups were conducted by counting (Fig. 1), and for later years when the shearing-sampling method was used (Fig. 2). Although the slopes varied substantially from year to year (they ranged from 71 in 1913 to 29 in 1963), the variance about the regression line within any particular year was very small.

We compared the various estimators and sampling plans by analyzing the bias and variance of the estimates and the half-width and coverage properties of nominal 95% confidence intervals for 3 years (1965, 1970, 1975) of data when all rookies were sampled. Detailed statistics on the performance of the estimators under all sampling plans appear in a manuscript report available from the authors[3].

Under simple random sampling, the "blow-up" estimate is unbiased. The various ratio estimates are all slightly biased (in most cases less than 1%) with the regression estimate exhibiting the largest degree of bias. In Figure 3 the percentage of bias of the three ratio estimates for the 1975 data is shown as a function of sample size (under simple random sampling). Estimates based on 1975 data were the most biased among the 3 years analyzed, and these biases are exhibited as a worst case. The regression estimate was the most biased, and for these data the bias increased as the sample size increased; however, the bias was only about 1% and is not serious.

Confidence intervals were constructed for each subsample and a count was made of the number of nominal 95% confidence intervals containing the "true" population. The observed coverage was near 95% for most procedures. Confidence intervals for the regression estimate tended to be conservative, i.e., a higher than 95% coverage rate, while the coverage rate for the ordinary ratio estimate tended to be less than 95%. Coverage rates for the jackknife and blow-up estimates were near 95% or a bit higher. This indicates that the estimate of the variance of the regression estimate tended to be too large, that of the ordinary ratio estimate was too small, and that the estimates of the variance of the blow-up and jackknife estimates tended to be unbiased. The half-widths of confidence intervals for the ratio estimates were nearly equal. All were less than one-half the length of the half-width of the confidence interval of the blow-up estimate.

The rookeries were stratified by population size. Two methods for stratifying the rookeries were investigated: one using two strata (small and large rookeries) and the other using three strata (small, medium, and large rookeries). As in the case of simple random sampling, the ratio estimators were superior to the blow-up estimates. The estimators under the three-strata sampling plans were less variable than under the two-strata sampling plans. In addition, the computed levels of the nominal 95% confidence intervals were higher and the size of the confidence intervals smaller. Under the three-strata sampling plans, the standard deviations of the estimates were about 10% smaller than under simple random sampling with the same size sample. This resulted in a similar reduction in the size of the confidence intervals. These results indicated that reasonable estimates of the size of the pup population can be made using any of the ratio estimators under various sampling plans. The superior plans use three strata: two small, one medium, and one large rookery; one small, two medium, and one large

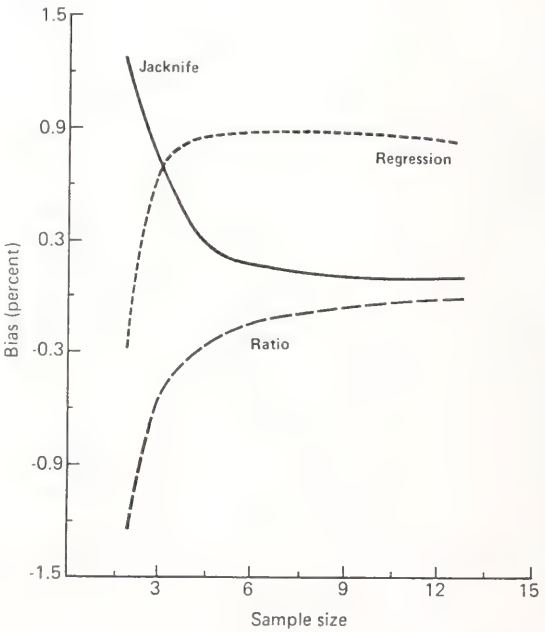

FIGURE 3.—Percent bias of the jackknife estimates (___), ordinary ratio estimates (· · ·), and regression estimates (– – –) based on simple random sampling of 1975 northern fur seal data.

[3]York, A. E., and P. Kozloff. 1985. Estimation of numbers of fur seal pups born on St. Paul Island, 1980-84. Unpubl. manuscr. Available National Marine Mammal Laboratory; 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 28th Annual Meeting of the Standing Scientific Subcommittee of the North Pacific Fur Seal Commission, March-April 1985, Tokyo, Japan.)

rookery; and, one small, one medium, and two large rookeries.

A subsampling estimation procedure was developed for 1980-84: rookeries were grouped into three strata—large, medium, and small rookeries; one small, one medium, and two large rookeries were sampled each year. Furthermore, in order that some rookeries were not disturbed inordinately more than others, each rookery was sampled at least once, but no more than twice during the 5-yr period. We had intended to census all rookeries in 1985, but logistic difficulties permitted a sampling of only seven rookeries.

A summary of data collected during 1980-86 with the ordinary ratio, jackknife ratio, and regression estimates of the ratio of pups to breeding males appears in Table 2. The estimates based on the three methods are approximately equal within each year; in most cases, the jackknife estimate lies between the ordinary ratio and regression estimates. Estimates of the total number of pups born were obtained by adding counts of dead pups to number of pups alive at the time of census (based on jackknife ratios); approximate 95% confidence intervals were calculated (Table 2).

In Figure 4, estimated 95% confidence intervals

TABLE 2.—Summary of the total number of breeding northern fur seal males, ratios of the number of pups alive at the time of sampling to the number of breeding males counted, estimated number of pups alive at the time of sampling, counted number of dead pups, and estimated number of pups born, and approximate 95% confidence interval based on the jackknife standard errors, St. Paul Island, 1980-84.

Year	Total no. of breeding males	Ratios of pups to breeding males			Number of pups		
		Jackknife ratio	Ordinary ratio	Regression	Live	Dead	Born
1980	5,490	35.695	35.896	35.580	195,966	7,859	203,825 ± 36,838
1981	5,120	33.720	33.821	33.563	172,646	6,798	179,444 ± 20,054
1982	5,767	34.035	33.896	34.147	196,280	7,301	203,581 ± 9,665
1983	4,827	33.135	32.766	33.448	159,944	5,997	165,941 ± 19,216
1984	4,803	34.803	33.861	34.167	167,159	6,115	173,274 ± 22,531
1985	4,372	40.482	40.292	41.071	176,992	5,226	182,258 ± 18,887
1986	4,603	34.735	34.936	34.498	167,656	7,771	167,656 ± 16,272

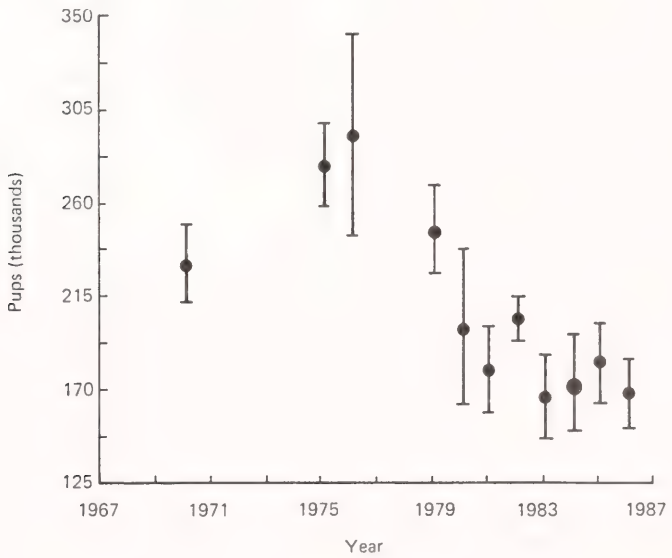

FIGURE 4.—Approximate 95% confidence intervals and estimates of numbers of northern fur seal pups born on St. Paul Island, AK, 1970-86. (We include only those years for which data were available to compute estimates according to the methods developed in this paper.)

of numbers of northern fur seal pups born on St. Paul Island since 1970 are presented; estimates for 1970-79 are based on data from Lander (1980). We computed estimates for those years in which censuses were made on all rookeries or for which data were available to compute estimates according to the methods developed in this paper. Regressions of logarithms of numbers of pups born versus time indicated a statistically significant decrease during 1975-81—a decrease of 7.5% per year with a standard error of 2%. During 1981-86, there is no statistically significant decreasing or increasing trend; the estimate of the slope is −1.8% with a standard error of 1.8%. This slope is statistically different from the −7.5% slope calculated for 1975-81 ($P > 0.90$).

DISCUSSION

Our study indicates that we can obtain reasonable estimates of the total number of northern fur seal pups born from subsampling as few as four rookeries of St. Paul Island if estimates of numbers of pups and breeding males are available for the sample rookeries and if a total bull count is available for the island. Subsampling is successful because within a given year, pup production is predictably proportional to numbers of breeding males. Some refinements in the reduction of bias and variance can be made by restricting the subsamples to stratified designs over large, medium, and small rookeries.

The advantages of subsampling rookeries for censusing northern fur seal numbers are considerable. Most important is the reduction of total disturbance on the northern fur seal population on the island. Our sampling schedule over several years attempts to apportion disturbance approximately equally so that rookeries are neither under- or oversampled through time. This is an important aspect of the sampling design, since it is not known how great the long-term impact of disturbance is. In addition, subsampling requires a smaller crew for the shearing and less time for resampling, resulting in considerable savings of resources.

Ratios of numbers of males to pups, and consequently breeding females, vary considerably over time, even in successive years. It is difficult to interpret the meaning of these changes. During the period covered by Figure 1 (1912-22), numbers of pups born on St. Paul Island were increasing rather rapidly. Since males begin to breed at an older age than females, part of the increase in the ratio of breeding males to pups may be explained by the number of breeding males lagging a few years behind the number of breeding females. Significantly different ratios from one year to the next could also be due to differences in counting methods or abilities among individual counters, or to different survival rates among separate cohorts (e.g., harvest rates). Figures 1 and 2 also imply a certain consistency and a rather uniform rate of usage of rookeries by breeding males and females, in that, if a rookery accounts for 10% of breeding males within a year, it will account for approximately 10% of the total pup production within the same year. A rookery's relative contribution to both these populations may change but the correlation between them does not appear to change.

The recent history of the population of numbers of pups on St. Paul Island in Figure 4 shows a decrease of about 7.5% per year during 1975-81. No significant trend is detectable after 1981, although the number born in 1982 was significantly higher than in 1981 or 1983-86. The causes of the decline are unknown. There is no evidence that pregnancy rates have changed significantly since the 1950's (Goebel and Gentry 1984[4]). Thus, considerable attention has centered on potential causes of increased mortality of northern fur seals: entanglement in debris (e.g., Fowler 1985), effects of weather (Trites 1984; York 1985[5]), and direct effects on food availability from competition with fisheries in the North Pacific Ocean (York and Hartley 1981; Swartzman and Harr 1983; Kajimura 1984; Loughlin and Livingston 1985[6]). One may also speculate that the pattern of decline and possible stabilization in numbers of pups born resulted from a new disease which abated or was controlled by an immune response of the population (c.f., Geraci et al. 1982).

Of the aforementioned explanations for the decline, only entanglement has been cited as a major contributing factor with an attributed mortality of

[4]Goebel, M. E., and R. L. Gentry. 1984. The use of longitudinal records of tagged females to estimate fur seals survival and pregnancy rates. Unpubl. manuscr. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 27th Annual Meeting of the Standing Scientific Committee of the North Pacific Fur Seal Commission, March-April 1984. Moscow, U.S.S.R.)

[5]York, A. E. 1985. Forecast of the 1985 harvest on St. Paul Island. Unpubl. manuscr. National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115. (Background paper submitted to the 28th Annual Meeting of the Standing Scientific Subcommittee of the North Pacific Fur Seal Commission, March-April 1985, Tokyo, Japan.)

[6]Loughlin, T. R., and P. A. Livingston (editors). 1986. Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985. NWAFC Processed Report 86-19, 92 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

about 5.5% per year (Fowler 1985). It is possible that entanglement in debris was indeed responsible for the decline during 1975-81, however, the data in Figure 4 do not seem to support this hypothesis. If entanglement were the principal cause of this decline, we would have expected the population to have continued to decrease at the pre-1981 rate since the observed entanglement rates have remained stable since 1976.

We may never know the cause of the 1975-81 decline in northern fur seal production. In general, estimates of population size are highly variable so several censuses are required to detect a statistically significant decrease in a population; thus, the fact of a decline, unless it is sudden and dramatic, is not usually known for several years following its initiation. Post facto studies are invariably subject to criticism for flaws in experimental design; thus, careful continual monitoring of the many aspects of the biology of a population is the best hope for ascribing a particular cause to a population change. Comparisons of the population dynamics, food habits, incidence of diseases, and entanglement rates of northern fur seals with other pinniped species which share their habitat in the North Pacific Ocean might shed additional light on the various hypotheses.

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LABORATORY STUDIES OF THE PATTERN OF REPRODUCTION OF THE ISOPOD CRUSTACEAN *IDOTEA BALTICA*

The isopod *Idotea baltica* is a cosmopolitan species that can be an important component of fishes' diets in the field (summarized in Sywula 1964 and Strong and Daborn 1979). Tinturier-Hamelin (1963) reported that *I. baltica* extends along all European coasts, from Finland to Gibraltar, including Great Britain; it is present in the Baltic, the Mediterranean, and the Black and Caspian Seas. In North America it is present from Nova Scotia to North Carolina. In addition, Sywula (1964) reported that it is also found in South America, Bermuda and Barbados, the Red Sea, Australia, New Zealand, and Java.

Investigators who have observed *I. baltica* in the field have reported the species' association with the dominant plants of the community. Interestingly, the type of associated plant varies with geographic locality. In Nova Scotia it is found on *Ascophyllum nodosum* (Strong 1978), in the Baltic on *Fucus vesiculosus* (Salemaa 1979), in Poland on *Zostera* (Mobius 1873, as reported in Sywula 1964), and on *Ulva lactuca* in Jamaica Bay, NY (present study). Generally, the animals' principal food is the plant on which they are found, and this species is often the principal primary consumer of its community (Strong and Daborn 1979), occupying a critical link in local fish food chains.

The present study was undertaken to provide information about *I. baltica*'s reproductive behavior and physiology under laboratory conditions in order to determine the feasibility of developing it as a fish food for mariculture systems.

Materials and Methods

All animals were collected in July and August 1985, by removing attached *Ulva lactuca* thalli from the fouling community attached to submerged piers at the Barrens Island Marina, Jamaica Bay. The animals were sorted from these collections in the laboratory, and placed in individual 22.5 cm diameter glass culture dishes of ambient seawater (29 ppt) either in heterosexual pairs (30 pairs), or in isosexual pairs (20 male and 20 female isosexual pairs). The pairs were maintained at room temperature ($\bar{x}$ = 24.3 ± 2°C SD), with a light cycle of 15:9 L:D. They were fed *Ulva lactuca* thalli ad libitum. These pairs were observed 2 times a day, 12 hours apart, in the light, and maintained until one of the members of the pair died. Observations consisted of noting the occurrence of molts and ovulations, as well as any reproductive behaviors exhibited.

Intermolt periods were calculated by counting the number of days between the first and second molts only of animals maintained in heterosexual pairs. This was done to minimize any artifacts of culture conditions.

In addition to the pairs, 60 females were isolated in individual 10 cm diameter culture dishes. These females were used to determine the variability in timing of molts, ovulations, and expression of reproductive behavior. Females were observed at 12-h intervals, and the dates and times of their molts noted. Males were introduced either on the day the females molted, on day 1 or day 2 after the molts, or no males were introduced at all (12, 19, 13, and 16 different females observed, respectively). The occurrence and timing of copulations, ovulations, and subsequent brood developments were noted for all four groups of females.

Finally, to determine the timing of copulation with respect to the sequence of the shedding of the two parts (see following section) of the female's exoskeleton, males were introduced to five females between the first and second partial molts and the males' responses noted.

Results

Molts

Intermolt periods.—Individuals of both sexes molted repeatedly until they died. Some females molted four times in succession. The average intermolt period of the females was 13.4 ± 0.8 SD days (n = 17, range = 12-15 days); for the males it was 13.0 ± 4.4 days (n = 15, range = 7.5-23.0 days). There was no significant difference between the sexes (Student's t-test; t = 0.24, df = 30, $P > 0.05$).

Nature of the molts.—The exoskeleta of both sexes were cast off the same way. First the posterior half of the exoskeleton (from the fifth segment back) was shed, then the remaining anterior portion was cast off. The anterior part included the first four pairs

of oostegites of the female's brood pouch; the posterior part included the fifth and last pair. There was an interval between the shedding of the two parts (females: $\bar{x}$ = 6.5 ± 6.1 SD hours, n = 35, range = 0-12 hours; males: $\bar{x}$ = 8.3 ± 6.9 SD hours, n = 36, range = 0-24 hours). There was no significant difference between the intervals of the two sexes (Student's t-test: t = 1.41, df = 69, $P < 0.05$). Finally, the observations suggest that there is no terminal molt in either sex, because all individuals molted until they died.

Amplexus

Males picked up and held onto females until the females molted. During amplexus, females were held ventral to the male, and only the males' movements resulted in locomotion. There was no specialized point of attachment on the female. The male inserted the angle formed by the dactyl held slightly extended from the palm of its second gnathopod into the space between the curved, lateral edges of the female's first and second pereonal segments. Sometimes males held onto females with posterior pereiopods as well, but this was only for brief periods of time.

The occurrence of amplexus was correlated principally with female intermolt stage. Amplexus began about $\bar{x}$ = 1.9 ± 1.4 SD days before the female molt (n = 15, range = 0.0-4.5 days) and all couples separated within 12 hours after the female discarded its anterior cast. Thus, females were in amplexus for approximately the latter 14.2% of their intermolt periods.

Most females were in amplexus 24 hours before their posterior molts and separated from the males 24 hours after their anterior molts (Table 1; Fisher's exact probability test, $P < 0.001$). In contrast, most males were not in amplexus either before or after their molts (Table 1; 83.3% and 64.3% not in amplexus before and after the molt, respectively). However, there was a significantly greater proportion of males in amplexus after than before their molts (χ^2_1 = 3.94, $P < 0.05$). Thus, amplexus was principally correlated with female intermolt stage, but male intermolt stage had an affect as well.

Finally, amplexus was never observed in either male or female isosexual pairs.

Copulations

During copulation the male held the female's body in a perpendicular, ventral position, and inserted its pleopods into the posterior part of the female's brood pouch about five times in rapid succession. This was followed by a rest period of about 5 seconds during which the male retained its hold on the female. Then the sequence was repeated two or three more times.

Copulations occurred within minutes after males were introduced to females that had shed both parts of their exoskeleta, regardless of how many days ago the molt had occurred. In contrast, no copulations occurred in the five females that had just molted the posterior portions. Amplexus was initiated with these females instead, and copulation occurred only after the anterior portion of the exoskeleton was shed.

Ovulations

Isolated females ovulated about 2.9 ± 0.5 SD days after their molts (n = 14, range = 2-3.5 days). In contrast, females maintained with males in heterosexual pairs ovulated $\bar{x}$ = 0.12 ± 0.2 SD days after their anterior molts (n = 26, range = 0-0.5 days). The difference was significant (Student's t-test: t = 25.92, df = 38, $P < 0.001$). Another difference between isolated females and females maintained in heterosexual pairs was that none of the broods of the former group developed, while most of the latter broods did (Table 2: 0 of 14 vs. 24 of 26 broods, respectively; Fisher's exact probability test: $P < 0.001$). Eggs ovulated by isolated females were no longer observed in the brood pouches about 5.0 ± 1.8 SD days after the females' molt (n = 12, range = 3-6 days) or about 2.0 ± 1.5 SD days after ovula-

TABLE 1.—Frequencies of occurrences of amplexus 12 hours before the posterior molt and 12 hours after the anterior molt in *Idotea baltica* maintained in heterosexual pairs.

		Before		After	
Sex	Number of molts	Number in amplexus	Number apart	Number in amplexus	Number apart
Females	33	31	2	1	32
Males	42	7	35	15	27

TABLE 2.—Frequencies of ovulations and viable broods of isolated females and females paired with males.

		Number of		Number of ovulated broods that	
	No. of females	ovulations	no ovulations	develop	do not develop
Isolated females	16	14	2	0	14
Paired females	26	26	0	24	2

tion (n = 12, range = 0.5-5.0 days). These observations show 1) that females ovulate in the absence of a male, but 2) delay their ovulations under those conditions; and 3) such eggs disappear from the brood pouches a few days after ovulation.

The introduction of a male to a female any time during the approximately 3-d period that females could delay their ovulations stimulated ovulation. Copulations generally occurred within 5 minutes after males were introduced to females 0, 1, or 2 days past their molts, and all ovulations occurred within 3 hours of copulation. There was no significant difference in the frequencies of copulations and ovulations among females isolated for different lengths of time (Table 3; $\chi^2_2 = 0.008$, $P > 0.05$ and $\chi^2_2 = 0.712$, $P > 0.05$ for copulations and ovulations, respectively).

In contrast, the broods of females who copulated and ovulated 0 and 1 day after their molts developed significantly more often than did the broods of 2-d postmolt females (Table 3; $\chi^2_1 = 3.61$, $P < 0.05$). This suggests that unfertilized eggs aged past 2 days have reduced viability.

TABLE 3.—Frequencies of copulations, ovulations, and viable broods of isolated females introduced to males 0, 1, and 2 days past the females' molts.

Days after molt	No. of females	Number of Copulations Yes	Copulations No	Ovulations Yes	Ovulations No	Broods that develop Yes	Broods that develop No
0	12	10	2	10	2	10	2
1	19	16	3	14	5	12	7
2	13	11	2	11	2	5	8

Discussion

The present study has shown that males and females remain apart until towards the end of the female intermolt period, when amplexus is begun. This continues until the female molts, when copulation, followed by ovulation occurs. Females repeated this cycle in the laboratory until they died. Some females produced three broods in succession, without a rest period. In contrast, females in the field in Nova Scotia produce only one brood (Strong 1978), and in the northern Baltic most have one brood (although some may have two (Salemaa 1979)).

It is impossible to say whether the difference in the number of broods produced in the field and in the laboratory is caused by environmental and/or genetic differences. In support of the first explanation, a recent symposium has demonstrated the importance of photoperiod in regulating the timing of reproductive activities of marine animals (Marcus 1986), and, specifically, in the number of broods of some peracarids (Steele and Steele 1986). The photoperiod of Nova Scotia may limit the number of broods there. In support of the second explanation, Healy and O'Neill (1984) noted that two populations of *I. granulosum* produced different numbers of broods in Ireland and in Britain, although there was no significant difference in temperature or latitude at the two locations. Further, while Tinturier-Hamelin (1963) found no reproductive barriers among *I. baltica* from different parts of Europe that were hybridized in the laboratory, she did conclude that the subspecies were genetically distinct. Only laboratory culture, under identical conditions, of representatives from different geographic localities will reveal whether the difference in the number of broods is genetic.

The present observations also reveal that *I. baltica* females spend relatively little of their intermolt periods in heterosexual pairs (14%) compared with other peracarids (the mean of seven other peracarids was 32% (Borowsky 1986)). Strong (1978) reported that a short amplexus period was correlated with a high risk of fish predation in the amphipod *Hyallela azteca* and suggested that couples are more visible than single individuals. This may be the case here as well. Fish and predaceous shrimp are abundant in the community from which individuals for the present study were collected (D. Franz pers. commun.[1]).

Both sexes cast off the posterior parts of their exoskeleta before the anterior parts. Since the female's anterior portion includes most of the brood pouch, the new marsupium is not completely exposed until both parts are shed. Males did not copulate with females that had not molted the anterior cast. The sequence of molts and copulation makes sense, because the present study shows that copulations stimulate ovulations. If copulation occurred before the anterior portion of the pouch were shed, the new eggs might be secreted into the old brood pouch, and then discarded along with the anterior molt.

The present study reveals some flexibility in the timing of key reproductive events. Females could copulate until about 36 hours after they cast off their anterior molts without incurring a significant reduction in fecundity. However, if copulation did not occur by about 3 days after their molts, females

[1]D. Franz, Department of Biology, Brooklyn College, City University of New York, Bedford Avenue and Avenue H, Brooklyn, NY 11210, pers. commun. August 1986.

ovulated spontaneously. These eggs did not develop and disappeared from the brood pouches after a few days. Thus, there appears to be no sperm storage in *I. baltica*, and females must be accompanied by a male at the time of their molts to ensure the development of their broods.

One interesting observation was that males engage in amplexus significantly more often after than before their molts. This may be explained by the observation that neurons become detached from the exoskeleton a few days before the molt (Guse 1983). Thus, if contact and/or water-borne pheromones are secreted by receptive female *I. baltica* as they are in some other peracarid females (Borowsky 1984, 1985, 1986), it is possible that the males cannot sense the stimuli produced by females shortly before their own molts, and therefore are less likely to engage in amplexus at that time.

Conclusion

The results of the present study show that *I. baltica* adults can be maintained in the laboratory, and will reproduce freely with minimal effort and at minimal cost. Females fed exclusively on *Ulva lactuca* produced many broods in succession in nonaerated, uncycled water. While further study is necessary to determine whether juveniles will develop under these conditions, and, if so, what the yield will be, the observations reported here suggest the feasibility of culturing this species for fish mariculture systems.

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OCCURRENCE OF THE FIRST FRESHWATER MIGRATION OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM*, IN THE CONNECTICUT RIVER, MASSACHUSETTS[1]

Occurrence of a freshwater migration of the gizzard shad, *Dorosoma cepedianum* (Lesuer) (Clupeidae), is documented for the first time in a New England river system. Adult gizzard shad were observed and collected at the Connecticut River fishlift facility in Holyoke and upstream in Massachusetts during 1985 and 1986. It is believed that the Connecticut River migrants are derived from a population recently observed in Long Island Sound and already occurring in the Hudson and Connecticut River estuaries and Nantic Bay.

The gizzard shad is a widely distributed species occurring in marine and tidal freshwaters along the

[1]Contribution No. 104 of the Massachusetts Cooperative Fishery Research Unit, which is supported by the U.S. Fish and Wildlife Service, Massachusetts Division of Fisheries and Wildlife, Massachusetts Division of Marine Fisheries, and the University of Massachusetts.

middle, southern, and gulf coasts of eastern North America (Megrey 1979). Landlocked freshwater populations are known from the Mississippi River drainage (Miller 1956; Megrey 1979) and the Great Lakes (Miller 1956, 1960). On the North American Atlantic coast, the gizzard shad has been reliably reported north to northern New Jersey and New York Harbor (Breder 1938; Miller 1956) (Fig. 1).

Recent evidence indicates that the gizzard shad has ventured into the estuaries of certain major rivers draining into Long Island Sound. Dew (1974) reported that the species was first observed in the lower Hudson River estuary at Indian Point (river km 64.5) between 1969 and 1971 (Fig. 1). Subsequent surveys suggested that the lower Hudson River population is increasing and that reproduction was possibly occurring in the estuary (Dew 1974). However, George (1983) believed that the gizzard shad in the lower Hudson River are derived from fish which migrated through the Erie Canal to the Mohawk River and down the Hudson River. If George's (1983) theory is correct then the lower Hudson River population would have been founded by landlocked freshwater animals, and not by migrating "anadromous" adventives from New York Harbor.

Results and Discussion

In the Connecticut River, adult gizzard shad were first observed near the mouth (river km 2.4, Fig. 1) in 1976 by commercial fishermen using gill nets set for American shad, *Alosa sapidissima*, (Whitworth et al. 1980). In 1984 and 1985, gizzard shad

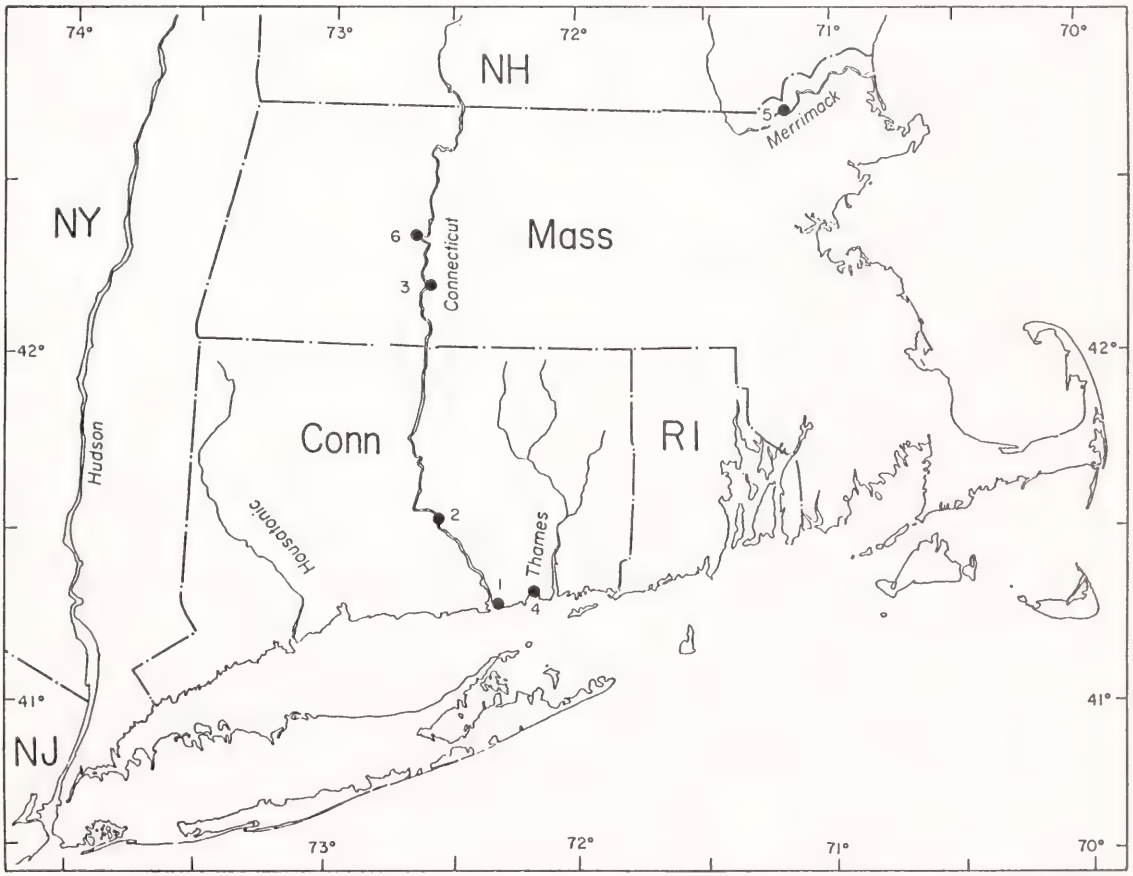

FIGURE 1.—Recent reports of the gizzard shad, *Dorosoma cepedianum*, in New England: 1. Whitworth et al. (1980), Connecticut River, river km 2.4. 2. Gephard (text fn. 2), Connecticut River, river km 26. 3. O'Leary and Smith (this paper), Connecticut River, river km 139.4. 4. Gauthier (text fn. 3), Millstone nuclear power plant. 5. S. Henry (Assistant Aquatic Biologist, Massachusetts Division of Fisheries and Wildlife, Field Headquarters, Route 135, Westboro, MA 01581), Lawrence fishway, Merrimack River. 6. O'Leary and Smith (this paper), Connecticut River, Northampton Oxbow, river km 150.

were subsequently collected by fishermen using gill nets farther up the Connecticut River estuary (river km 26; S. Gephard pers. commun.[2]; Fig. 1) and entrained at the Millstone nuclear power plant in Nantic Bay, CT (C. Gauthier pers. commun.[3]; Fig. 1). In October 1985, a single specimen was captured at the Lawrence fishway on the Merrimack River, Lawrence, MA. This specimen has been deposited into the Museum of Zoology, University of Massachusetts.

During late May and June of 1985 and 1986, over 70 subadult gizzard shad were observed at the Holyoke Dam Fishlift on the Connecticut River in Holyoke, MA (river km 139.4) approximately 69 km above the head of the tide (Fig. 1). Four live and one dead gizzard shad—two females, two males, and one unknown—were collected at the fishlift; all have been deposited into the Museum of Zoology, University of Massachusetts. Mean total length of the live fish was 418 mm (range 395-460 mm) and all were sexually mature. The mean total length of the live fish is near the maximum size reported for this species from freshwater (Miller 1960; Bodola 1965) and larger than the Mohawk River specimens discussed by George (1983). Later in July 1986, a single juvenile gizzard shad (50 mm TL) was captured in the Northampton Oxbow of the Connecticut River (river km 150, T. Savoy pers. commun.[4]; Fig. 1). The specimen is in the collections of the Connecticut Department of Environmental Protection. A follow-up survey in September by O'Leary at the same locality produced no juveniles, but two small adults (300 and 348 mm TL) were captured and these two specimens have been divided among the Museum of Zoology, University of Massachusetts and the Museum of Comparative Zoology, Harvard University. The collected juvenile specimen provides evidence that the species is breeding in the freshwater portion of the Connecticut River, and the co-occurrence of adults suggests that the Northampton Oxbow is an area where reproduction is occurring.

Cooper (1983) suggested that the gizzard shad has been extending its range northward along the east coast of North America in response to warming climate. Whether the species has moved into the Hudson River estuary (Dew 1974) while migrating northward or has entered the river from Lake Erie through the Mohawk River (Erie Canal) (George 1983) is unresolved. The species could have entered the Connecticut River only from the estuary as no inland connection between the Connecticut River and the Great Lakes or the Hudson River exists. The same argument would apply for the origin of other species encountered along the New England coast. The lack of any sightings of gizzard shad prior to 1985 at the Holyoke fishlift leads us to believe that the 1985 and 1986 migrations represent the first indisputable movement into freshwaters of gizzard shad from a marine stock occurring off the southern New England coast. These findings support Cooper's (1983) contention that the gizzard shad is extending its range northward along the eastern North American coastline.

[2]S. Gephard, Fishery Biologist, Marine Fisheries Office, State of Connecticut, Department of Environmental Protection, P.O. Box 248, Waterford, CT 06835, pers. commun. August 1985.

[3]C. Gauthier, Scientist, Northeast Utilities Environmental Laboratory, P.O. Box 128, Waterford, CT 06385, pers. commun. August 1985.

[4]T. Savoy, Fishery Biologist, Marine Fisheries Office, State of Connecticut, Department of Environmental Protection, P.O. Box 248, Waterford, CT 06385, pers. commun. August 1986.

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RELATIONSHIP OF OTOLITH LENGTH TO TOTAL LENGTH IN ROCKFISHES FROM NORTHERN AND CENTRAL CALIFORNIA

Knowing the relationship between otolith length and total length of a fish is useful for two reasons: 1) Fish size can be estimated from otolith lengths measured from otoliths encountered in predator stomachs, in core samples, archaeological sites, etc., and 2) the length of a fish can be verified when the age determined from the otolith lies outside expected values.

The otolith/total length relationship is useful in predator-prey and archeological studies if fish size can be extrapolated from otolith length. Otoliths are often the only part of a prey fish remaining in a predator's gut (Ainley et al. 1981; Treacy and Crawford 1981) or at cooking sites of archeological middens (Fitch 1972). Fish lengths could be estimated from otoliths found as remains of prey or in coastal archaeological excavations (Fitch and Brownell 1968). Existing keys (e.g., Morrow 1979) allow identification of fish species from otoliths. With these keys, personal reference collections, and the length relationships described in this paper, investigators will be able to verify species and size data collected in field sampling, and obtain more complete knowledge of prey species of marine mammals, birds, and fishes.

Large-scale surveys, such as the California cooperative survey (Sen 1984) that samples commercial rockfish landings in northern California, are prone to errors at several levels. Problems that may be encountered in collecting otoliths and measuring fish lengths include errors in recording lengths and the mixing up of otoliths. Some errors can be corrected by measuring the otolith and estimating the size of the fish it came from. Every effort should be made to eliminate erroneous data from the database before curves are constructed or cohort analysis is performed.

In this paper, I report the results of my investigation of the relationship between otolith length and total length for 30 rockfish species of the genus *Sebastes*. Linear regression statistics are presented for all fish of the species encountered.

Methods

Specimens were collected during a life history study on the rockfishes of northern and central California conducted at the Southwest Fisheries Center Tiburon Laboratory. Fish were sampled from the commercial trawl fishery, the commercial sport fishery, skiffs, and research cruises from 1977 to 1980. Specimens were identified to species, and then total lengths of frozen—then thawed—carcasses were measured on a meter board in millimeters (mm). Otoliths were measured to the nearest 0.1 mm with an ocular micrometer. The greatest length of the otolith was measured from the anterior tip to the most posterior projection (Kimura et al. 1979) (Fig. 1) as if the otolith were flat, without compensating for the curvature. Linear regressions were run on total length (y) versus otolith length (x) for 30 rockfish species. Outliers (± 3.0 standard deviations) from the line were assumed to result from measurement or recording errors and were discarded (2% of the observations).

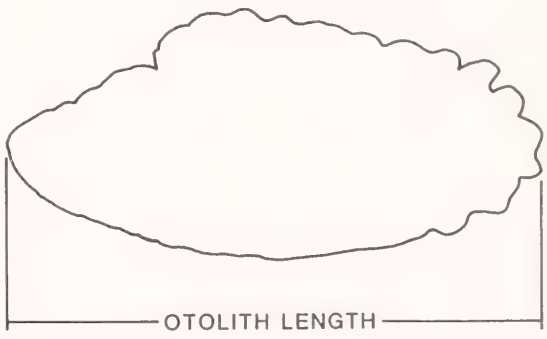

FIGURE 1.—The length of an otolith is measured from the anterior tip to the posterior projection.

Table 1 gives the sample size (N) and the minimum and maximum total lengths used in the analysis for each species and each sex. Table 2 shows estimates of y-intercept (a), slope (b), standard error of estimate ($S_{y.x}$), correlation coefficient (r), and F for each species and sex. Analysis of covariance was used to determine if separate lines for males and females significantly reduced the variance from a common line (Kleinbaum and Kupper 1978). Analysis of covariance was also used to test for significant differences in the relationship of otolith length to total length between the sexes at the $P = 0.05$ level and the $P = 0.01$ level (Table 2). The highest values of r and examination of scattergrams (Fig. 2) indicate that the length relationships are linear over the observed range of values. Limiting the application of these regressions to the ranges of observed values is advised.

TABLE 1.—Sample sizes and size ranges used in the linear regressions of total length versus otolith length for *Sebastes*. Measurements are in millimeters.

Species of *Sebastes*	Males			Females		
		Total length			Total length	
	N	Minimum	Maximum	*N*	Minimum	Maximum
auriculatus	34	257	477	44	179	523
aurora	27	203	378	44	230	398
carnatus	100	112	289	103	109	279
caurinus	67	281	507	65	135	542
chlorostictus	73	155	450	101	162	458
chrysomelas	72	162	256	94	141	268
constellatus	54	186	422	45	177	430
crameri	42	206	445	47	134	505
diploproa	34	125	343	44	131	381
elongatus	25	188	326	73	135	378
entomelas	38	245	464	68	284	524
flavidus	163	254	504	221	232	539
goodei	26	227	385	52	227	556
hopkinsi	13	119	195	46	134	294
jordani	118	147	281	65	160	321
levis	14	267	773	15	237	900
maliger	13	317	481	21	226	478
melanops	120	334	534	89	197	607
melanostomus	34	250	442	46	297	538
miniatus	64	328	644	35	360	691
mystinus	141	248	480	63	213	375
nebulosus	25	270	391	23	257	500
ovalis	18	228	355	66	241	456
paucispinis	46	287	733	40	296	786
pinniger	92	249	585	81	251	622
rosaceus	72	212	426	75	203	310
ruberrimus	52	257	695	50	245	678
saxicola	29	141	240	73	159	358
semicinctus	15	125	150	16	128	182
serranoides	60	235	469	70	229	528

Results and Discussion

Linear regressions were run on each sex in order to investigate possible sexual differences. In 17 of the 30 species investigated, the relationship between otolith length and fish length is significantly different between males and females (Table 2). Sexual size dimorphism has been observed in 11 of the 17 species in Table 2. These species (plus *S. alutus*) include most commercially and sport-caught rockfishes in the northeastern Pacific Ocean. The six species for which growth curves have yet to be con-

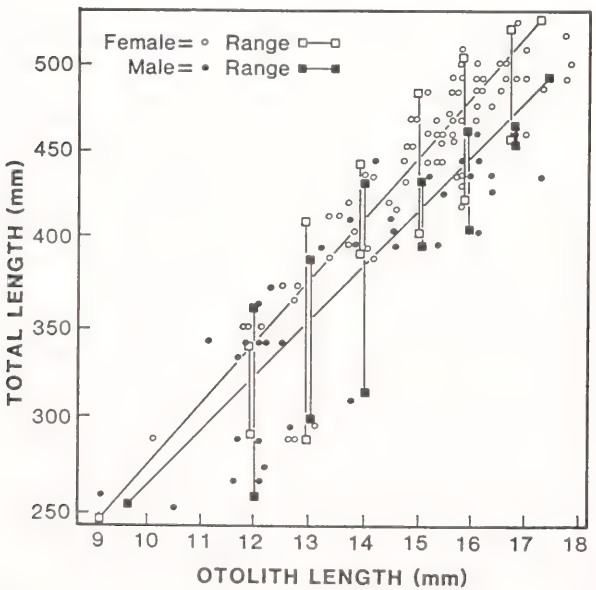

FIGURE 2.—Linear regression of total length on otolith length of widow rockfish, *Sebastes entomelas*. The range of values for males (•-•) and females (o-o) at each whole millimeter of otolith length.

TABLE 2.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes*. Measurements are in millimeters. The F-test was run using the sums squared from the analysis of covariance comparing males and females; * - P = 0.05, ** - P = 0.01.

Species of *Sebastes*	Males				Females				
	r	a	b	$S_{y.x}$	r	a	b	$S_{y.x}$	F
crameri[1,2]	0.926	19.270	24.629	22.054	0.988	−43.418	29.440	16.067	4.676*
diploproa[3,2]	0.980	1.282	21.090	12.686	0.985	−22.120	23.717	13.390	6.601**
entomelas[1,2,4]	0.871	−23.039	28.853	33.896	0.880	−51.835	32.452	28.968	6.243**
flavidus[1,2,5,6]	0.923	30.400	23.546	14.771	0.947	−12.604	26.901	18.389	25.637**
goodei[7]	0.975	1.696	23.866	12.741	0.987	−56.831	29.347	16.321	14.842**
hopkinsi	0.868	20.734	20.172	9.567	0.951	−10.895	26.890	10.999	9.172**
maliger	0.840	79.427	21.359	25.533	0.965	−105.649	33.479	19.259	4.221*
melanops[5,6]	0.912	5.472	27.070	18.456	0.949	−124.076	35.784	19.480	25.338**
melanostomus	0.907	−21.094	25.187	21.777	0.918	−21.713	26.211	23.405	8.441**
miniatus	0.961	−42.615	28.385	23.399	0.971	−72.278	30.607	24.103	4.638*
mystinus[6,7]	0.910	−2.255	28.987	23.112	0.881	60.010	22.054	14.965	3.643**
ovalis	0.903	26.185	24.964	13.268	0.963	−27.207	31.859	14.144	21.995**
paucispinis[1,8]	0.893	−51.911	38.441	55.433	0.931	−102.932	43.993	56.501	5.965**
pinniger[1,2,5]	0.950	−61.508	27.663	25.655	0.967	−95.891	30.455	29.004	8.200**
saxicola[1]	0.928	−0.111	19.074	7.544	0.974	−19.565	22.495	12.797	11.412**
semicinctus	0.880	34.331	16.015	4.061	0.938	12.022	21.372	4.981	20.081**
serranoides[6,9]	0.967	−5.307	25.898	13.462	0.969	−63.475	30.445	20.668	10.318**

[1]Westrheim and Harling 1975.
[2]Shaw and Archibald 1981.
[3]Boehlert and Kappenman 1980.
[4]Lenarz 1987.
[5]Six and Horton 1977.
[6]Wyllie Echeverria 1986.
[7]Miller and Geibel 1973.
[8]Wilkins 1980.
[9]Love and Westphal 1981.

structed may also show sexually size-dimorphic growth.

The 13 species with no difference noted between males and females consist primarily of two closely related taxonomic groups (Barsukov 1981). Few growth studies exist for these species. The first group of shallow, nearshore species is represented in this study by *S. auriculatus*, *S. carnatus*, *S. caurinus*, *S. chrysomelas*, and *S. nebulosus*. The growth curve for *S. chrysomelas* is the same for males and females (Zaitlan 1986). The second group is the subgenus *Sebastomus* (Chen 1971), represented in this study by *S. chlorostictus*, *S. constellatus*, and *S. rosaceus*. Growth curves exist for two members: *S. helvomaculatus* (Westrheim and Harling 1975) and *S. umbrosus* (Chen 1971), which do not show sexual size dimorphism. The indications are relationships of otolith length to total length reflect the age-at-length relationship between the sexes.

In food-habit studies, otoliths are often found but the sex and length of the fish are not known. Table 3 shows regressions for the combined sexes for those occasions when the sex is unknown or when the regressions were not significantly different between the sexes.

Data analysis for *S. entomelas* shows a potential to derive estimates of age from otolith lengths (Fig. 3). The calculated total lengths for males and females for each 1 mm increment in otolith length are overlaid on the age-length curve (from Lenarz 1987). These relationships are species-specific and

TABLE 3.—Results of linear regressions of total length (y) versus otolith length (x) for *Sebastes* for sexes combined. Measurements are in millimeters.

Species of *Sebastes*	r	a	b	$S_{y.x}$
auriculatus	0.968	−53.032	33.159	17.729
aurora	0.782	15.124	19.910	24.818
carnatus	0.945	−39.365	30.573	10.258
caurinus	0.906	5.099	30.234	26.291
chlorostictus	0.974	−18.537	24.113	14.898
chrysomelas	0.919	−21.780	28.609	9.020
constellatus	0.978	−37.484	25.266	13.123
crameri	0.971	−27.098	28.104	19.912
diploproa	0.980	−12.854	22.635	14.020
elongatus	0.974	−13.564	24.020	12.284
entomelas	0.898	−6.890	33.113	32.247
flavidus	0.938	−10.946	26.506	18.158
goodei	0.983	−57.996	29.129	17.819
hopkinsi	0.957	−30.546	28.868	12.168
jordani	0.985	−2.313	22.096	7.353
levis	0.973	−170.108	47.458	46.975
maliger	0.928	−53.107	29.967	23.862
melanops	0.930	−48.222	30.557	21.002
melanostomus	0.928	−47.070	27.362	23.590
miniatus	0.962	−56.738	29.365	24.516
mystinus	0.912	−18.175	29.765	23.204
nebulosus	0.891	32.970	25.181	16.131
ovalis	0.952	−53.472	33.562	17.179
paucispinis	0.903	−77.089	41.089	59.143
pinniger	0.957	−85.114	29.411	28.398
rosaceus	0.902	−83.484	22.533	10.908
ruberrimus	0.957	−76.233	31.328	31.206
saxicola	0.977	−32.765	23.399	12.663
semicinctus	0.924	−19.182	25.266	6.961
serranoides	0.965	−51.013	29.350	18.965

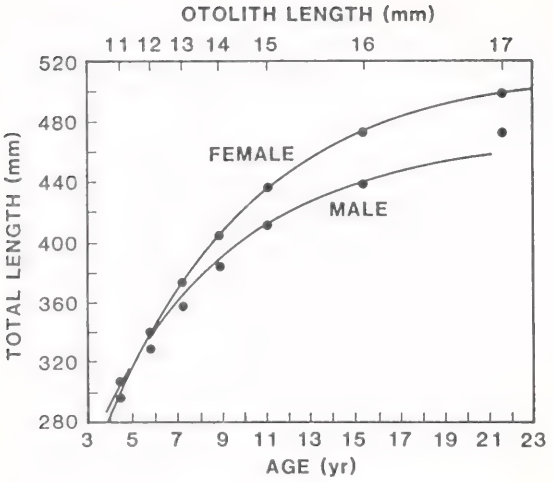

FIGURE 3.—Age-length curve for widow rockfish, *Sebastes entomelas* (from Lenarz 1987). The calculated total length from otolith length is overlaid on the curve to obtain an estimate of age.

should be used within well-defined limits. The scattergram (Fig. 2) with the mean and range of total length found at each 1 mm otolith length increment indicates the ranges within which these data are useful. Some problems in relating otolith length to age include the increased range of fish lengths at older ages and the observed thickening-instead of lengthening of otoliths in *Sebastes* (Boehlert 1985).

These results may be used to estimate total length from an otolith length as shown in the following example. If the otoliths are from fish of unknown sex, the regression statistics from Table 3 would be used to estimate fish length. If the otoliths are from fish of known sex, Table 2 would be consulted. If a species appears in Table 2, the regression statistics for the appropriate sex would be used to estimate fish length. If a species does not appear in Table 2, Table 3 (with regression statistics for males and females combined) would be used. For instance, to estimate fish length from otolith length (OL) for male *S. auriculatus*, the regression statistics from Table 3 are used. An otolith 10.0 mm long gives an estimated total length of

$$TL = a + b\,(OL)$$
$$TL = -53.032 + 33.159(10.0)$$
$$TL = 279 \text{ mm}.$$

Tables have been constructed with the regression statistics presented here. The table for each species (and sex, where appropriate) represents otolith lengths measured in millimeters and the corresponding estimated total length. These tables are available on request from the author.

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CRATER WOUNDS ON NORTHERN ELEPHANT SEALS: THE COOKIECUTTER SHARK STRIKES AGAIN

A variety of wounds are observed on northern elephant seals, *Mirounga angustirostris*. We report a new type of wound observed on juveniles, primarily from the Mexican islands west of Baja California and rarely from off California. The form and shape of these wounds, and their similarity to wounds reported from other marine mammals, fishes, and squids, suggest that they were caused by a small, squaloid shark of the genus *Isistius*, commonly known as the cookiecutter or cigar shark.

The shape of wounds, their location on the victim's body, the time of the year that the wounds are received, and the age of the seal provide a good indication of the cause. During the breeding season, for example, suckling seal pups bear bite marks on the snout, head, and rump, these having been inflicted by adult females (Le Boeuf and Briggs 1977). Weaned pups and adult females bear fresh bite marks of varying severity caused by adult males biting their necks while attempting to mate with them, and breeding-age males inflict a variety of bite wounds on each other during fights to establish dominance (Le Boeuf and Reiter in press). During winter and spring, *Mirounga angustirostris* of both sexes and all ages exhibit fresh wounds inflicted by white sharks, *Carcharodon carcharias*. The shape and serrated edges of those wounds are easily distinguished from the smooth-edged and halfmoon-shaped wounds caused by boat propellers (Le Boeuf et al. 1982; Tricas and McCosker 1984).

The wounds that we discovered were round, hollowed-out craters, smooth edged at the margin, about the size of a tennis ball, and unlike any of the wounds described above. The similarity in appearance of these wounds to scars inflicted by *Isistius* upon cetaceans (Van Utrecht 1959) and fishes (Jones 1971) implicate the cookiecutter shark as the probable cause. The only reported eastern Pacific occurrence of an *Isistius* is that of an *I. brasiliensis* from off the Galapagos (Compagno 1984). However, we have examined additional eastern Pacific specimens of *I. brasiliensis*, including a specimen from off Isla de Guadalupe.

Background information. Northern elephant seals inhabit traditional island and mainland sites from mid-Baja California, Mexico, to central California. Their range at sea along the Pacific coast is from Isla Cedros, Mexico, to the southern Aleutians. Feeding occurs beyond the continental shelf in deep water (Le Boeuf et al. 1986). It is not known how far from shore they go to feed, but some animals have been seen as far as 3,000 miles away on Midway Island in the mid-Pacific (Condit and Le Boeuf 1984). Several islands are used regularly throughout the year (Guadalupe, San Benito, Cedros, and Coronoados in Mexico and San Miguel, San Nicolas, Año Nuevo, and the Farallones); the sex and age composition of each colony varies with time of year (Le Boeuf and Bonnell 1980). Late August or early September, when most of the observations reported in this paper were made, is the end of the molt period for adult and subadult males and the beginning of the fall haul-out for juveniles, 1-4 years old. Breeding-age males, observed on land at this time, are completing the annual molt, a process that takes

30-40 days; they are in the process of returning to sea to feed. As their number declines, juveniles of both sexes begin to haul-out in increasing numbers. They have been at sea for 4 months or more. Census counts of total northern elephant seals are lower at this time than at any other time of the year (Le Boeuf and Bonnell 1980).

Observations and Methods

Most of the observations were made during an expedition to Mexican islands aboard the MV *Mirage* from 20 to 31 August 1986. Islands surveyed included Isla de Guadalupe, Islas San Benito, Cedros, San Martin, and Los Coronados. We censused northern elephant seals at all sites and, in doing so, recorded the incidence of fresh wounds. On 2 September 1986, we censused and recorded wounds on northern elephant seals at Año Nuevo Island off central California. Similar observations and censuses were conducted weekly at Año Nuevo Island during October and November, when peak numbers of juveniles are observed.

Censuses and inspection for wounds were made from an inflatable 6 m boat, approximately 10 m from seals lying on sandy beaches near the water's edge, or from on foot to get closer to the animals. When possible, we inspected both sides of all seals; we made no attempt to turn animals over to inspect the ventrum or to arouse them to better inspect them for wounds. Approximately half of the animals counted were seen from only one side. Thus, the counts of wounded animals we present are clearly underestimates of the true figure. We noted the location of all wounds and estimated their size and freshness.

We examined preserved specimens of *Isistius* housed in the Marine Vertebrates Division of the Scripps Institution of Oceanography (SIO).

Results

We observed fresh wounds on 20 juvenile northern elephant seals on three of the five island groups inspected in August and September (Table 1); there were no elephant seals on Isla San Martín. Four additional wounded juveniles were observed on Año Nuevo Island later in the year. All wounds were fresh, as indicated by their bloody color, and, with one exception, they were of similar size and shape (Fig. 1). The wounds were round and hollowed-out craters; the margin of each wound was smooth. Each wound was about 5-6 cm wide and 3-5 cm deep. One wound, although like the others in most respects, had a flap of skin and blubber still attached. No fresh crater wounds were observed on adult and subadult males.

Most animals had one wound. Wounds were located on various parts of the body (Fig. 1): the side posterior to the flippers, on the ventrum or the back and to either side or on the midline, on the chest and neck, and just behind the ear. Two animals had two wounds and one had three. One animal had two fresh, identical wounds on the dorsal midline at the level of the foreflippers, separated by approximately 3 cm. Another had two wounds 0.3 m apart on its left side. One animal had three wounds: two on the abdomen and one on the ventral surface of the neck.

The incidence of fresh wounds was highest on northern elephant seals inhabiting Isla de Guadalupe (8.4% of the juveniles censused) followed by Isla Cedros and Islas San Benito (Table 1). No wounded

TABLE 1.—Proportion and percentage of fresh crater wounds on northern elephant seals censused on various Mexican and Californian islands during August and September 1986.

Date	Island	Beach or islet	Adult and subadult males	Juveniles
21-24 Aug.	Guadalupe	Pilot Rock Beach	0/34 = 0	7/95 = 7.37
		Barracks Beach	0/19 = 0	3/35 = 8.57
		Twin Canyons	0/10 = 0	6/61 = 9.84
		Sum: all beaches	0/63 = 0	16/191 = 8.38
25-27 Aug.	San Benito	Este	0/10 = 0	1/57 = [1]1.75
		Centro	0/38 = 0	1/127 = 0.79
		Oeste	0/6 = 0	0/51 = 0
		Sum: all islets	0/54 = 0	2/235 = 0.85
28-29 Aug.	Cedros		0/13 = 0	2/45 = 4.44
31 Aug.	Los Coronados		0/1 = 0	0/14 = 0
2 Sept.	Año Nuevo		0/23 = 0	0/200 = 0

[1]Over 90 juveniles were counted but only 57 were observed close enough to document wounds.

animals were observed on Los Coronados during August or on Año Nuevo Island during August and September. However, four juveniles with fresh wounds, among 700 juveniles present, were observed on Año Nuevo Island during four censuses in November (1, 9, and 30 November). One animal, sighted on 1 November 1986, was marked; a 22-mo-old juvenile born on Año Nuevo Point on 11 February 1984 and tagged 1 month later.

As mentioned above, through examination of the holdings of the Scripps Institution of Oceanography Fish Collection, we uncovered additional Pacific specimens of *Isistius brasiliensis*. The eight specimens from seven lots included six males and two females. The largest, a 470 mm (standard length) female (SIO 69-345) with jaw width of 38 mm, was collected by IKMT (Isaacs-Kidd midwater trawl) between the surface and 2,000 m from north of Easter Island (lat. 25°58.5′S, long. 108°50.7′W). Another eastern Pacific specimen (SIO 78-183) is from off Isla de Guadalupe (29°26.5′N, 119°44′W) and was collected by phytoplankton net. The other eastern Pacific specimen (SIO 52-413) is from west of the Galapagos (00°00″, 100°00″W) and was captured at the surface by dip net.

Discussion

The fresh crater wounds we observed on juvenile northern elephant seals resemble those reported on beaked whales, sperm whales, several species of porpoises, and most of the baleen whales (Mackintosh and Wheeler 1929; Van Utrecht 1959), as well as those from a variety of pelagic fishes (Jones 1971) and a nuclear submarine (Johnson 1978). Jones (1971) and others have demonstrated conclusively that those wounds are the result of bites inflicted by the small squaloid shark, *Isistius brasiliensis*, or possibly by its congener, *I. plutodus*. To date, the only Pacific record of *I. plutodus* is from off Okinawa (Compagno 1984), so we therefore presume that the more wide-ranging and topotypical *I. brasiliensis* is the culprit. *Isistius brasiliensis* is epipelagic to bathypelagic and is known from all tropical oceans, extending northward to off Japan and Baja California and southward to Lord Howe Island. It is typically caught by midwater trawl at depths between 85 and 3,500 m; however, it is occasionally found at the surface at night. The shark is thought to be a diurnal vertical migrator, perhaps traveling a distance as great as 2,000-3,000 m in each direction; in so doing, it apparently encounters feeding *Mirounga*. As noted by Compagno (1984, p. 94), *Isistius* is highly specialized as a facultative ectoparasite in its dentition, suctorial lips, and modified pharynx that allow it to attach to the side of large prey, drive its sawlike lower jaw teeth into the skin and flesh of its victim, cut a conical plug of flesh, and then pull itself free with the plug cradled by its scooplike lower jaw and held by the hooklike upper jaw teeth. The scar patterns of juvenile *Mirounga* support the scenario described above. A comparison of jaw width of *Isistius* of known size with the scar patterns observed on *Mirounga* suggests that the attacking sharks were at least 50-60 cm long.

Northern elephant seals would appear to be easy prey for *Isistius*. They are slow swimmers, compared with large pelagic fishes, and they spend 85% of their time at sea underwater at depths of 400-650 m (LeBoeuf et al. 1985; Le Boeuf et al. 1986). Juvenile seals that use Isla de Guadalupe during the fall are evidently most prone to being parasitized. Juvenile seals hauling out on other islands, especially those to the north, are evidently not exposed to *Isistius* to the same degree. Until recently, no fresh crater type wounds were observed on seals at Año Nuevo despite 16 years of observations by B. J. Le Boeuf. Some wounds observed may have been old, healing crater type wounds, suggesting that the animals bearing them may have been immigrants from the south, the predominant direction of dispersal (Bonnell et al. 1979). Fresh crater wounds have not been observed on the northern elephant seals at the Farallones since their breeding began in 1972 (H. Huber, pers. commun.[1]). Le Boeuf never observed fresh crater wounds on northern elephant seals breeding on San Miguel and San Nicolas Islands during 1968-78, despite annual visits to these islands.

Mexican northern elephant seals of juvenile age fall prey to *Isistius* shortly before they haul-out in late August. Le Boeuf and coworkers never observed crater wounds on seals at these Mexican rookeries during the winter breeding season (13 visits since 1968) or summer molt (4 visits). The juveniles may be exposed to *Isistius* while feeding or while returning to the island. The marked difference in distribution of shark wounds is consistent with the observation that Mexican, southern Californian, and central Californian juveniles feed in different locations, and each "subpopulation" feeds north of its birthplace (Condit and Le Boeuf 1984). Juveniles, trapped in fishing gear, have been caught around 200 m below the surface and captured 16-224 km offshore.

[1]H. Huber, Point Reyes Bird Observatory, 4900 Shoreline Highway, Stinson Beach, CA 94970.

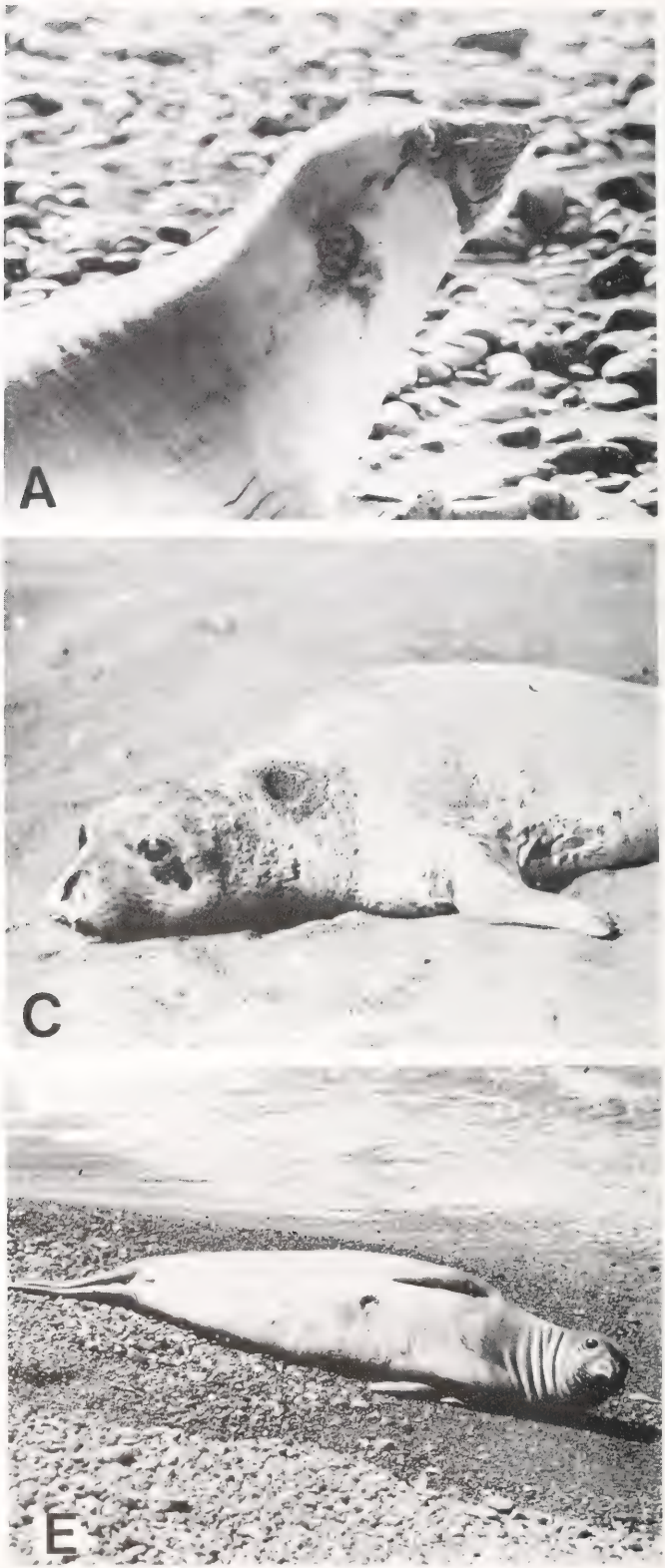

FIGURE 1.—Representative wounds on *Mirounga angustirostris* caused by *Isistius* attacks. A, B, C—taken at Isla de Guadalupe, Mexico; D, E—taken at Isla Este, Islas San Benito, Mexico; F—taken at Año Nuevo Island, California. Not visible in F are two other healing wounds along the animal's right flank. (*Photos A-E by B. J. Le Boeuf; photo F by P. Thorson.*)

B

D

F

That only juvenile northern elephant seals exhibit fresh crater wounds may be explained in several ways. It suggests that this age category is the only one exposed by depth or location to feeding *Isistius*; or, it may suggest that older age classes are able to avoid attack. Another interesting hypothesis concerns the common prey of both *Isistius* and *Mirounga*, midwater squid. It has been speculated that the bioluminescent pattern of *Isistius* might simulate the pattern of a large midwater squid and thereby attract squidophagus predators (Jones 1971) upon which it could prey. It seems unlikely that an *Isistius* could outswim a *Mirounga*; attacks by the shark would thus be accomplished either by attracting the seal, perhaps for a closer inspection of the shark, or by attacking the seal by stealth and surprise. The location of attack scars on the head region of *Mirounga* would indicate a frontal approach, whereas the scars on the back and flanks might indicate that the seal was unaware of the impending attack. Both scenarios are likely. It is also possible that juveniles seals are more readily attracted to the display of *Isistius*, not having learned yet to distinguish them from squid. Further insight into these hypotheses will be provided as more data concerning the spatial and temporal distribution of *Isistius* are collected.

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PHASE DIFFERENCE BETWEEN CALCIFICATION AND ORGANIC MATRIX FORMATION IN THE DIURNAL GROWTH OF OTOLITHS IN THE RAINBOW TROUT, *SALMO GAIRDNERI*

YASUO MUGIYA[1]

ABSTRACT

The relative role of calcium and organic matrix deposition in the formation of daily increments in otoliths was studied in in vitro preparations of otolith-containing sacculi of rainbow trout, *Salmo gairdneri*. Sacculi were incubated in a Ringer solution containing both ^{45}Ca and ^{3}H-glutamic acid for 2 hours at 6-h intervals throughout a 24-h period and then the uptake of these isotopes was determined for both otolith and saccular tissue fractions. Serum calcium and sodium concentrations were also analyzed for diurnal variations.

Serum calcium concentrations varied diurnally by 8% in a single phasic pattern, reaching a peak at dusk (1600 h) and a nadir at night (2200 h), while sodium concentrations remained almost constant throughout a 24-h period. Diurnal variation in the otolith's uptake of calcium and glutamic acid showed discrete, antiphasic cycles. The rate of calcium uptake varied in a pattern closely resembling that of serum calcium (the peak at 1600 h and the nadir at 2200 h); glutamic acid uptake remained almost constant during the daytime and peaked at night (2200 h). The results indicate that in rainbow trout daily increments of otoliths are formed by the antiphasic deposition of calcium and organic matrix.

Teleost otoliths consists of calcium carbonate in aragonite form and an organic matrix in which acidic amino acids dominate (Degens et al. 1969). Concentric rings within the microstructure of otoliths are commonly laid down on a daily basis (Campana and Neilson 1985; Jones 1986). A unit increment comprises one light and one dark ring when observed under transmitted light. These bipartite structures are also observable by scanning electron microscopy. After etching with weak acids or decalcification with calcium-chelating agents, they usually appear as an alternating pattern of well-calcified zones with elongated crystals perpendicular to the otolith periphery (accretion zone) and narrow grooves which intersects the crystal development at right angles (discontinuous zone). However, some recent studies (Mugiya and Muramatsu 1982; Watabe et al. 1982; Takahashi 1982; Morales-Nin 1987) showed that if the etching and subsequent treatments were carried out carefully, the organic matrix could be preserved in the discontinuous zone, appearing as a raised ridge. After complete decalcification of the otolith, Dean et al. (1983) and Radtke and Targett (1984) observed incremental features in the remaining matrix. Thus, stated in relative terms, the accretion and discontinuous zones appear to be alternatively calcium-dominant and matrix-dominant structures. However, Watabe et al. (1982) observed that morphologically similar matrix material extended continuously between accretion and discontinuous zones, and proposed a possible mechanism for otolith increment formation. For their recently proposed model, Campana and Neilson (1985) also assumed continuous matrix formation in diurnal otolith growth.

Based on these morphological studies, three hypotheses might account for the formation of the bipartite structure of otolith increments: 1) both organic matrix and calcium deposition show diurnal variations occurring in antiphase, 2) calcium deposition varies diurnally, while matrix deposition does not, and 3) calcium deposits at a constant rate throughout a 24-h period, while matrix deposition varies diurnally. All these would result in the formation of alternate zones where calcium or matrix deposition predominated. Of these, the last possibility can be excluded. Physiological studies indicate that the rate of calcium uptake by otoliths varies diurnally in goldfish and rainbow trout (Mugiya et al. 1981; Mugiya 1984).

The present study was undertaken to investigate diurnal variation in matrix formation and to

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relate its phase, if apparent, to otolith calcification. Because diurnal variations in otolith calcification show seasonality (Mugiya 1984), an ideal way to examine such a phase relationship is to determine the rates of calcium and matrix deposition on a single otolith simultaneously, using a double-tracer method and in vitro, isolated sacculi from rainbow trout. Diurnal profiles of glutamic acid and calcium uptake were examined in the otoliths and the remaining saccular tissue. Serum calcium and sodium concentrations were also measured for diurnal variations.

MATERIALS AND METHODS

Rainbow trout, *Salmo gairdneri*, 29-31 cm in standard length, were obtained from a commercial dealer and reared in a pair of outside ponds supplied with 14°C running water. They were fed trout food pellets once a day at around 0845 h. Two females showed maturing ovaries, so their data were omitted. No males were excluded because maturing testes have little, if any, effect on the level of serum calcium. The experiment was carried out in December 1984. Dusk occurred at 1600 h and dawn at 0700 h.

At each sampling time, five or six fish were gently netted one at a time. Blood was immediately collected from the caudal vessels by cutting the tail of the fish and draining it into test tubes. After centrifugation, the separated sera were stored at −30°C for 6-24 hours and analyzed for calcium and sodium concentrations by flame photometry using an atomic absorption spectrophotometer (Hitachi[2] 518).

After blood collection, the head was severed, trimmed, and placed in an oxygenated Ringer solution kept at 14°C. The sacculi were dissected under a binocular microscope according to a previously described technique (Mugiya 1984). The pair of sacculi were placed in the incubation medium, and the next fish was netted. Time was recorded to ensure that sacculi from each fish were incubated for the same length of time.

Isolated sacculi were placed in a glass vessel and incubated in 50 mL of a Ringer solution (Mugiya 1986) containing ^{45}Ca and ^{3}H-glutamic acid (New England Nuclear) at concentrations of approximately 0.17 μCi/mL and 0.33 μCi/mL respectively. The incubation was carried out with oxygenation at 14°C for 2 hours. To determine proper incubation times, the uptake of ^{3}H-glutamic acid by otoliths was plotted against time; although in this preliminary experiment, sacculi were incubated for periods of up to 3 hours, steady-state levels were obtained in less than 2 hours.

After incubation, sacculi were rinsed several times in the radioisotope-free Ringer solution and separated into otolith and saccular tissue fractions under a binocular microscope. The separated otoliths were lightly rinsed in water, placed in individual counting vials, dried at 90°C overnight and then weighed. The saccular tissue was directly placed in the vial without a further rinse and air-dried. These samples were solubilized in a mixture of 0.2 mL perchloric acid and 0.2 mL hydrogen peroxide at about 80°C for 2 hours, and added to Scintisol EX-H (Wako) for counting (liquid scintillation spectrometer, Aloka LSC-673).

Tritium and ^{45}Ca activities were measured simultaneously using two channels with narrowed windows, 50-300 for ^{3}H and 70-900 for ^{45}Ca. Although the amount of ^{3}H activity entering the Ca channel was found to be practically negligible, ^{45}Ca would certainly affect counts on the H channel, despite the window conditions. Therefore, counts on the H channel were corrected by the equation:

$$^{3}H \text{ activity} = H - 1/\alpha \, Ca \qquad (1)$$

where H and Ca represent counts on the H and Ca channels respectively, and α (contamination ratio) is experimentally defined as $\log \alpha = 0.1386R - 0.0488$ where R is a ratio determined for the quenching level of each sample. The validity of this correction was further checked by another equation based on differences in the physical half-life of the isotopes:

$$^{3}H \text{ activity} = \frac{Ca_0H_2 - Ca_2H_0}{Ca_0 - Ca_2} \qquad (2)$$

where H_0 and Ca_0 are counts on the H and Ca channels at time 0 respectively, and H_2 and Ca_2 are those recounted a few months later. Because these two methods of discrimination gave essentially the same results, the data from Equation (1) were presented in this study.

Some rainbow trout have an aberrant otolith in either or both of their sacculi (Mugiya 1972). If

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

the highly aberrant form was found by inspection after incubation, it was excluded from the data.

RESULTS

Serum calcium concentrations varied diurnally by approximately 8% in a single phasic pattern (Fig. 1). The maximum level (5.47 meq/L) occurred at dusk (1600 h), followed by a rapid decrease ($P < 0.05$) to a nadir (5.04 meq/L) at night (2200 h). The level then gradually increased toward the next peak. In contrast, serum sodium concentrations showed a statistically insignificant variation of only 0.6% ($P > 0.05$; 148.1-149.0 meq/L) throughout a 24-h period.

When otolith-containing sacculi were incubated with ^{3}H-glutamic acid, the saccular tissue (without otoliths) was almost saturated with the isotope within the first 30 minutes or hour of incubation (Fig. 2). Otoliths also showed a considerable uptake (about 60% of the total) of the isotope in the first 30 minutes, followed by a gradual increase in radioactivity until 3 hours, when the incubation was terminated. Tritium activities were always 6-8 times higher in the saccular tissue than in the respective otolith (Fig. 2). The time-related uptake of ^{45}Ca by these tissue fractions has been reported (Mugiya 1984). In that study, the saccular tissue was saturated with ^{45}Ca within the first hour of incubation, while otoliths showed an almost linear increase in ^{45}Ca uptake during the first 5 hours at which point the incubation was terminated.

The uptake of calcium by otoliths varied diurnally (Fig. 3), and the pattern was quite similar to that of diurnal variations in serum calcium concentrations (Fig. 1). The rate of calcium uptake was intermediate at 1000 h, peaked at dusk (1600 h), and then decreased significantly ($P < 0.02$) by 37% to a nadir at night (2200 h). The low rate persisted through the night, increasing slightly at 0400 h. Clearly otolith calcification proceeded more actively during the daytime. The uptake of glutamic acid by the same otoliths also showed a diurnal variation, and its profile was almost antiphasic to that of calcium uptake (Fig. 3). The rate of the uptake remained rather low during the daytime with a small nadir at dusk (1600 h). Then the rate increased significantly ($P < 0.05$) to a peak at night (2200 h), followed by a return to the daytime level. Thus the most active deposition of otolith matrix (at least proteins) occurred during the first half of the nighttime period, when calcium deposition was at its lowest level.

The uptake of glumatic acid by the saccular tissue showed significant ($P < 0.02$), diurnal

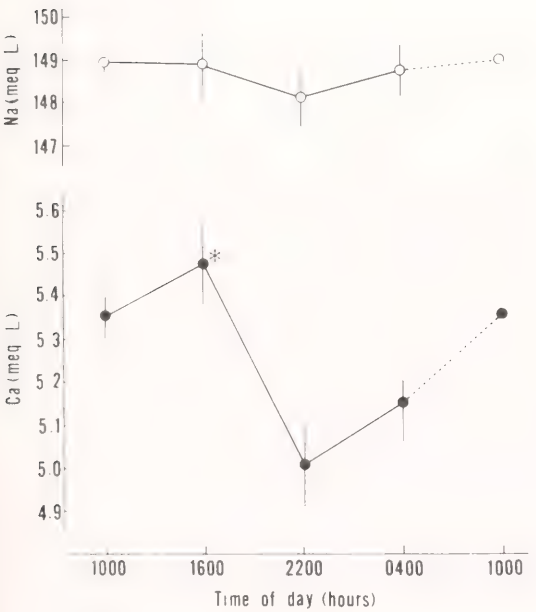

FIGURE 1.—Diurnal variations in serum calcium (●) and sodium (○) concentrations in rainbow trout. Each plotted value represents mean ± SE of 5 or 6 fish. *$P < 0.05$ for 2200 h.

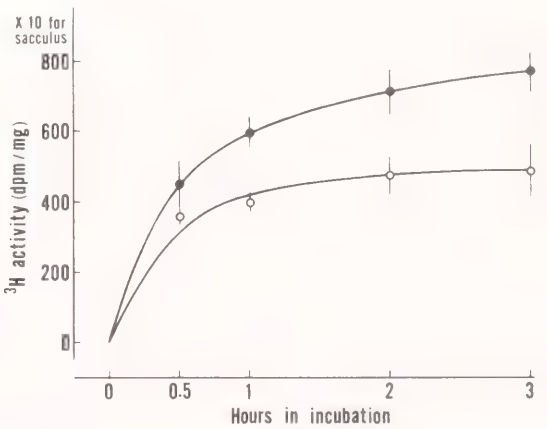

FIGURE 2.—Time course for the in vitro uptake of ^{3}H-glutamic acid by otoliths (●) and the saccular tissue (○) of isolated sacculi in rainbow trout. The radioactivity of the saccular tissue is expressed as dpm per otolith weight (mg) because the dry weight of the individual saccular tissue was too light to be determined accurately. Each plotted value represents mean ± SE of 8-10 samples.

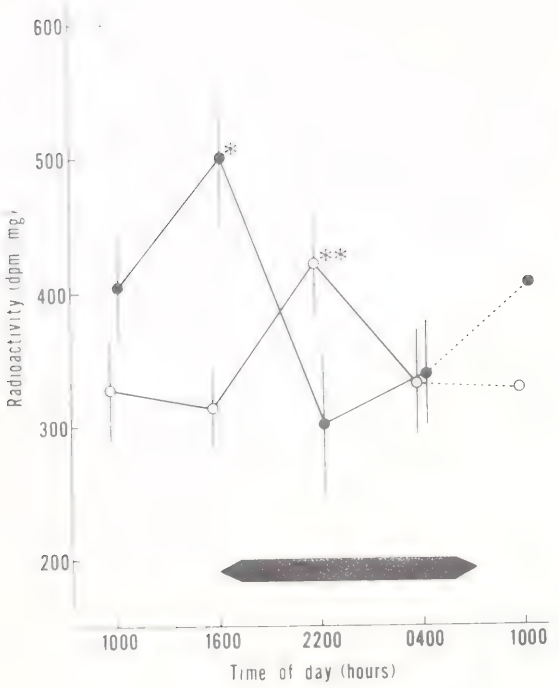

FIGURE 3.—Diurnal variations in the in vitro uptake of ^{45}Ca (●) and ^{3}H-glutamic acid (○) by otoliths in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. Dark horizontal bar indicates nocturnal and twilight periods. $*P < 0.02$ for 2200 h; $**P < 0.05$ for 1600 h.

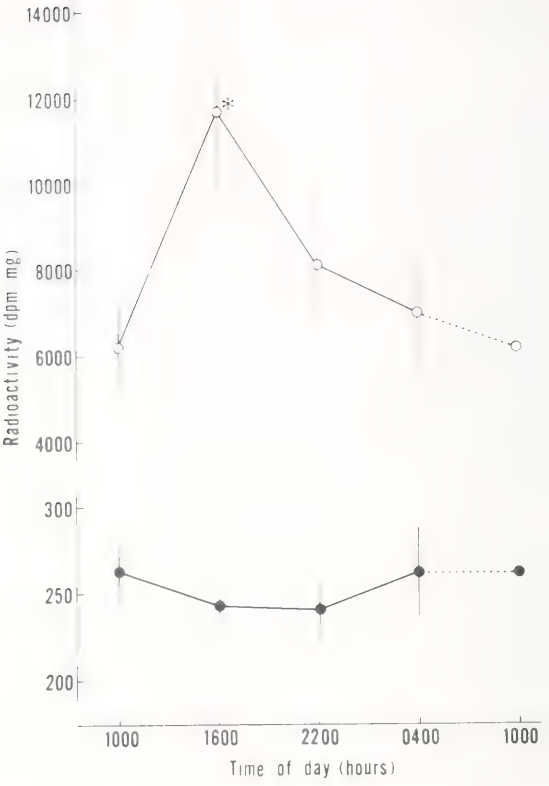

FIGURE 4.—Diurnal variations in the in vitro uptake of ^{45}Ca (●) and ^{3}H-glutamic acid (○) of saccular tissue in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. $*P < 0.02$ for 1000 h.

variation with a single peak at 1600 h when matrix deposition on the otoliths was lowest (Fig. 4). Note that the active biosynthesis of matrix proteins in the saccular tissue is not necessarily followed by their instantaneous deposition on the otoliths, suggesting the presence of cyclic secretion activity in the cells of the sacculus. The rate of calcium uptake by the saccular tissue did not vary much throughout a 24-h period (Fig. 4).

Ratios of counts of ^{45}Ca and ^{3}H-glutamic acid in the respective otoliths magnified the antiphasic relationship between ^{45}Ca and ^{3}H uptake (Fig. 5). Significant variation ($P < 0.01$) between the peak (1600 h) and the nadir (2200 h) demonstrates the much greater deposition of calcium relative to glutamic acid during the daytime, which suggests that in December the accretion zone forms during the daytime with its peak at dusk.

DISCUSSION

Although previous studies (Mugiya et al. 1981; Mugiya 1984) showed that otoliths grew by the diurnal deposition of calcium, it remained to be determined whether matrix deposition on the otoliths was diurnal or not. Histochemically, otolith matrix consists of various kinds of substances such as proteins, acid mucopolysaccharides, PAS-positive materials, and lipids (Mugiya 1968). Of these, proteins are the most dominant component and are characterized by a high content of acidic amino acids (Degens et al. 1969). In the present study the diurnal deposition of otolith matrix was evident when examined in terms of the incorporation of glutamic acid into otoliths, showing a single peak at night. Interestingly, calcium deposition on the same otoliths proceeded most actively at dusk, followed by minimum deposition at night. Thus, it is concluded, in rainbow trout kept under natural photoperiod, the pace of otolith calcification is almost antiphasal to the pace of matrix deposition on the otoliths.

The present results, where both calcium and

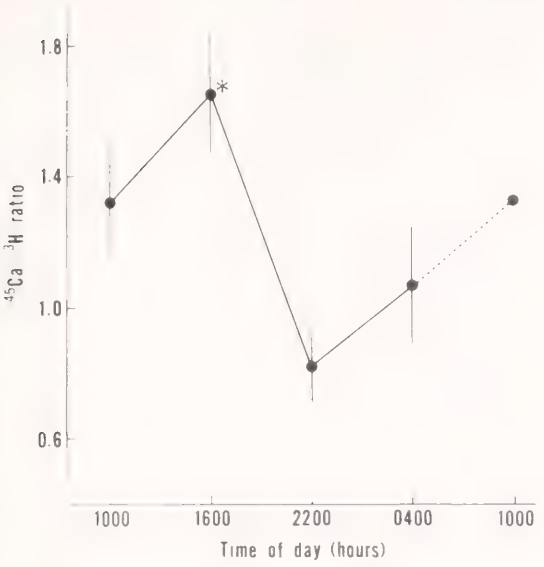

FIGURE 5.—Diurnal change in the ratio of ^{45}Ca to ^{3}H-glutamic acid activity incorporated into the same otoliths in rainbow trout. Each plotted value represents mean ± SE of 8-10 samples. *$P < 0.01$ for 2200 h.

matrix deposition on otoliths varied diurnally in antiphase, indicate the relative importance of these substances for daily increment formation in otoliths. The accretion zone is formed predominantly by calcium deposition, while the discontinuous zone results from reduced calcium and substantially increased matrix deposition on the otoliths. These findings coincide with the morphological observation that the accretion zone is a crystalline layer with organic materials and the discontinuous zone is a layer containing more organic materials and less calcium (Mugiya and Muramatsu 1982; Watabe et al. 1982). Watabe et al. (1982) observed that the matrix fibers and their aggregates were morphologically similar in the two zones and continuous throughout in *Tilapia* and *Fundulus* otoliths. Based on these observations, they have suggested that the matrix materials are identical in the zones and their deposition might be an uninterrupted event during diurnal otolith growth. They also stated that this did not necessarily imply that the rate of organic matrix secretion was diurnally constant. In fact, the present study reveals that diurnal variations in the rate of the matrix deposition, coupled with variations in calcium deposition, play an important role in otolith increment formation.

Although the sacculus contains the otolith, otolithic membrane, and endolymph, a high content of acidic amino acids is characteristic of the calcified otolith (Degens et al. 1969). Therefore, variations in the uptake of glutamic acid by the saccular tissue should be closely related to the activity of the matrix formation of the otolith, even though glutamate is also used as a neurotransmitter in the saccular macula (Potter et al. 1986). Otolith forming cells, yet to be positively identified (Mugiya 1974; Dale 1976; Dunkelberger et al. 1980; Saito 1984), synthesize the precursor of the matrix and secrete it into the lumen. The precursor may then deposit on the otolith after further biochemical modification.

The present study showed the presence of a time-lag between the matrix biosynthesis in the saccular tissue and its deposition on the otoliths. However, this does not necessarily mean that these two processes are separated in phase. In this study, calcification and matrix formation were measured in terms of "instantaneous" growth rates (Ottaway 1978). Therefore the maximum deposition of organic matrix on otoliths at night must be accompanied by the active biosynthesis of the matrix in the cellular level and its consecutive secretion into the lumen, which may rather reduce the radioactivity in the saccular tissue. The high radioactivity in the tissue at dusk might result from the accumulation of the newly synthesized matrix owing to the reduction of its transport to the otoliths. These results suggest the presence of at least three different phases in otolith matrix formation: the active synthesis of matrix proteins on the cellular level with its reduced deposition on the otoliths, active synthesis with active deposition, and inactivity in both synthesis and deposition.

Mugiya (1984) reported that the profile of diurnal otolith calcification was antiphasal between the summer and winter solstices in rainbow trout. In the winter experiment, the peak and the nadir of calcium deposition on otoliths came at 1600 h and 0400 h, respectively; while in the present winter experiment the peak at 1600 h decreased to the nadir earlier, at 2200 h, followed by a slight increase at 0400 h. Although there is a difference in the time-related profiles, the results of both experiments mainly showed that otolith calcification slowed down after the onset of darkness and remained relatively inactive until the next sunrise.

Molluscan nacre shows a laminar structure resulting from alternate accumulation of organic

matrix and calcium carbonate crystals. In the development of these bipartite structures, matrix deposition on growing crystals is known to interrupt further crystal growth (Wilbur 1980). This results in the alternate formation of calcium-rich and matrix-rich layers. In such cases, the matrix may have opposite functions in controlling crystal growth: as an inhibitor for the crystal growth along the C-axis and as a nucleator for the formation of the next crystal layer (Crenshaw 1982). The matrix appears to play a key role in controlling the formation of these different layers. Although this sequence is likely to be the case for otolith increment formation (Wilbur 1980), the rate of calcium deposition on otoliths appears to be closely related to the level of serum calcium, which is regulated by the action of hypercalcemic and hypocalcemic hormones (Oguro and Pang 1982). Serum calcium has been suggested as a trigger for otolith calcification through the calcium-calmodulin system (Mugiya 1986). Although Pickford (1953) found that hypophysectomy resulted in no otolith growth in killifish, what exactly controls the rate of matrix deposition on otoliths remains unknown.

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ESTIMATES OF THE LANDED CATCH OF RIGHT (AND OTHER WHALEBONE) WHALES IN THE AMERICAN FISHERY, 1805-1909

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ABSTRACT

Using a combination of the numbers of bowhead, right, humpback, and gray whales listed for particular voyages by C. H. Townsend, and the declared returns of whale oil and whalebone from the same voyages as listed by A. Starbuck and R. B. Hegarty, mean oil and whalebone yields per whale are calculated and temporal trends in these yields investigated for each species. These are then used to obtain an estimate of the total landed catch for each 5-year period from 1805 to 1909, using the species composition from Townsend's lists and adjusting it upwards from the ratio of oil or bone production for Townsend's sample to the total known importation of these products to the United States for the same period. An alternative estimate is based on the catch per voyage in Townsend's sample, stratified by voyage-type (sperm, whalebone, or mixed), and prorated up by the number of whaling voyages of the same type as listed by Starbuck and Hegarty. The two methods produced estimates of the landed catch by American-registered vessels between 1805 and 1909 of 29,748-30,313 bowhead, 70,325-74,693 right, 14,164-18,212 humpback, and 2,665-3,013 gray whales.

Between 1715 and 1928, whaling vessels from American ports are estimated to have made 13,927 voyages, mostly under sail, in their worldwide pursuit of oil and whalebone (Sherman 1965). In 1846, at the peak of the fishery, the American whaling fleet comprised over 735 vessels displacing 233,189 tons (Hohman 1928). Because of the essentially unregulated and competitive nature of the enterprise, no systematic recording or collection of catch statistics was ever initiated for this very extensive fishery.

In 1875, Alexander Starbuck began to compile a list of the returns of whaling vessels from American ports from 1715, a task continued to the end of the fishery in 1928 by Hegarty (1959). These publications list for each voyage the vessel's name, class, tonnage, captain, managing owner or agent, destination, dates of sailing and arrival, and the results of the voyage in barrels of sperm or whale oil and pounds of whalebone. Numbers of whales taken are not given, but this did not prevent Starbuck (1878) from making his own calculations. In a footnote to his table J, which listed quantities of oil and whalebone imported into the United States from 1804 to 1876, Starbuck stated that

> Scammon estimates that sperm whales will average 25 and right whales 60 barrels of oil, and of the former 10 and of the latter 20 per cent of those killed are lost. Upon that basis the above amounts of oil would represent the slaughter of 225,521 sperm, and 193,522 right whales.

The latter figure has frequently been quoted as representing the size of the historical take of right whales (sometimes incorrectly for the period 1804 to 1817, an error apparently originally perpetrated by Harmer [1928], who also inferred that the entire take was of southern right whales). It is clear however that the landings of oil not only included production from both northern and southern right whales, but also from bowhead, humpback, and gray whales, species for which Starbuck (1878) made no allowance in his original calculation.

In this paper, an attempt has been made to revise Starbuck's calculations to account for the species composition of the catch, to extend his analysis forward in time using importation figures provided by Hegarty (1959), and to use whalebone as well as oil production. An independent method of estimating the landed catch using the catch per voyage has also been developed.

The motivation for this paper arose from the International Whaling Commission meeting on the past and present status of right whales, held in Boston in 1983, where the need for an improved estimate of the size of the American catch of right whales became apparent (Brownell et al. 1986).

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MATERIAL AND METHODS

From logbook extractions, Townsend (1935) tabulated the numbers of sperm, bowhead, right, humpback, and gray whales taken per voyage by 744 whaleships (mostly American) between 1751 and 1925. These figures include not only the whales processed but also those killed and brought alongside but subsequently lost before processing; these statistics have thus been termed the "landed catch" in this paper. The numbers of right whales are listed by ocean (i.e., North and South Pacific, North and South Atlantic, and Indian Oceans). In all, 53,877 whales are listed from 1,665 voyages. Excluding non-U.S. vessels, 16,837 baleen whales were taken in a total of 1,651 voyages, of which 636 were only sperm whaling voyages. The species composition of the baleen whale catch as extracted by Townsend has formed the basis of all the analyses performed in this paper, and is henceforward referred to as the "Townsend sample".

Some of the original work sheets used by Townsend in his 1935 paper were discovered in 1978 in the library of the Osborne Laboratory of the New York Aquarium. These comprise voyage abstracts giving the date, ocean, geographical position, number, and species of each whale landed, together with remarks such as "found dead", "cow and calf", etc.; about half of the work sheets are in the original handwriting of the compiler(s), while the remainder consist of typewritten copies. The abstracts cover voyages by most vessels whose names started with letters A through J (bark *A. Houghton* to brig *Juno*). Because some errors apparently occurred between the original abstracts and the final printed version (Schevill and Moore 1983), the catch data for the 438 voyages on which baleen whales were landed and for which abstracts were available has been checked against the figures tabulated by Townsend (1935). Errors were found in 32 voyages (or about 7% of the total) and corrected. The abstracts examined represent a landed catch of 6,982 baleen whales, or roughly 41% of the total Townsend sample.

Mean oil and whalebone yields per whale have been obtained by comparing the numbers of whales caught on a voyage (as listed by Townsend) with the amount of whale oil or whalebone landed for the same voyage (as listed by Starbuck (1878) or Hegarty (1959)). To avoid complications created when more than one baleen whale species was taken, only voyages where a single baleen whale species was taken have been analyzed. Because of suspected differences in size (and so presumably in yields of products) between North Pacific right whales and those from other seas (Omura 1958), they have been considered as a separate "species" for the purposes of this section. In order to reduce the amount of variation in yield and to avoid situations where Townsend seems to have had access to only a partial log of the voyage, only voyages on which 10 or more animals of that species were taken have been used (or roughly 20% of Townsend's sample of voyages on which whalebone whales were taken). Oil or bone sent home or sold abroad has been included where it is known; as Starbuck (1878) has pointed out, that sold abroad was not always accounted for.

Figures for the total annual importation of oil and whalebone into the United States have been taken from Starbuck (1878) and Hegarty (1959).

For the catch per voyage analysis, the voyages in the Townsend sample have been stratified according to type, either sperm (when only that species was landed), whalebone (when no sperm whales were included in the catch), or mixed (when both sperm and whalebone whales were taken). The numbers of such cruises have then been adjusted upwards by the numbers of such voyages found in the Starbuck/Hegarty compilation, where vessels were identified as sperm whalers if they were reported as returning with or sending home only sperm oil, as whalebone whalers if they only reported whale oil and/or bone, and as mixed whalers if they returned with or sent home both whale oil/bone and sperm oil. Two additional classes were recognized in the Starbuck/Hegarty compilation: "clean" voyages and "incomplete" voyages. Clean voyages were those entered as such by Starbuck (1878), but as Hegarty (1959) did not continue this practice, any of the voyages he listed that were completed but for which no production was reported were scored as "clean". Both authors listed several voyages that were not completed owing to fire, shipwreck, the vessel being condemned, etc., and for which no production was reported. These voyages were scored as "incomplete", and half their number was allocated on a prorata basis as either sperm, whalebone, mixed, or clean whalers, based on the proportions of these categories in the sample of completed voyages. The other half of the incomplete voyages was discarded, the assumption being that such voyages were on average probably half as successful as those completed and that Townsend (1935) was unlikely to have had access

to the logbooks of many of them. Incomplete voyages comprised 9.6% of those listed by Starbuck (1878) and Hegarty (1959).

A "plus minus" figure following any estimate refers to one standard error.

Values given for the coefficient of variation (CV) have been obtained using variances calculated by the jackknife method (using one voyage as the sampling unit). No attempt has been made to calculate coefficients of variation for the final estimates because 1) certain independent components of the variance could not realistically be assessed (e.g., variation in the proportion of a particular species in the total catch to that in the Townsend sample from one 5-yr period to the next) and 2) any biases in the data are likely to be of greater magnitude than statistical errors resulting from sampling variation.

ESTIMATES BASED ON PRODUCTION

The number of baleen whales landed by American whalers as extracted by Townsend (1935) is listed by five yearly period in Table 1. If Townsend's data for a particular voyage covered more than one calendar year, the catch would be entered against the later date, as this was more likely to correspond to the importation figures used as a basis for reconstruction of the catch. A total landed catch of 4,963 bowhead, 8,293 right, 2,879 humpback, and 569 gray whales was recorded for the period 1805-1914.

Average Oil Yield Per Whale

Right Whales

There were 147 right whale cruises producing oil yields ranging from 22.5 to 219 barrels (Fig. 1). As expected, the 17 voyages that took North Pacific right whales had higher yields (83 to 219 barrels) than the 130 taking right whales elsewhere (22.5 to 150 barrels), and so have been considered separately.

There was no significant trend in oil yield per whale during the period in which North Pacific right whales were taken ($b = -1.15 \pm 0.91$, $t = 1.27$, $P > 0.20$), so the overall average oil yield per whale of 41,645/341 or 122 barrels (CV = 0.063) has been used. This compares with published averages of 125 barrels, males making 60 to 100 and females 100 to 250 barrels (Clark 1887a), and 130 barrels (Scammon 1874).

There appeared to be a distinct decline in the oil yield of right whales on other grounds after 1882 ($b = -1.09 \pm 0.30$, $t = 3.60$, $P < 0.02$). Oil yields after this date have therefore been calculated from the least squares estimating equation fitted to the data:

$$y = 64.78 - 1.090\ (x - 1882)$$

TABLE 1.—Five-year compilation of whalebone whale catches from Townsend (1935).

Period (arrival)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl.	Pac.	Ind.			
1805–1809	—	—	—	43	—	—	—	—	43
1810–1814	—	—	—	—	—	—	—	—	—
1815–1819	5	—	—	3	22	—	2	—	32
1820–1824	—	—	—	81	—	—	—	—	81
1825–1829	—	—	—	269	—	—	1	—	270
1830–1834	—	—	—	940	71	72	5	—	1,088
1835–1839	—	—	—	761	356	477	96	—	1,690
1840–1844	—	—	324	53	516	505	66	—	1,464
1845–1849	91	—	1,088	55	349	129	89	—	1,801
1850–1854	1,101	—	165	88	34	48	84	6	1,526
1855–1859	1,238	1	235	53	72	83	242	65	1,989
1860–1864	650	9	117	109	104	48	193	205	1,435
1865–1869	717	2	107	108	25	43	124	215	1,341
1870–1874	471	—	15	45	18	46	774	70	1,439
1875–1879	104	6	13	54	1	13	380	[illegible]	579
1880–1884	119	4	1	77	26	—	619	—	846
1885–1889	76	5	38	53	72	3	171	—	418
1890–1894	86	—	3	38	13	—	22	—	162
1895–1899	183	1	12	7	—	6	10	—	219
1900–1904	74	—	6	11	—	2	1	—	94
1905–1909	33	—	1	10	6	71	—	—	121
1910–1914	15	—	—	26	—	25	—	—	66
Total	4,963	28	2,125	2,884	1,685	1,571	2,879	569	16,704

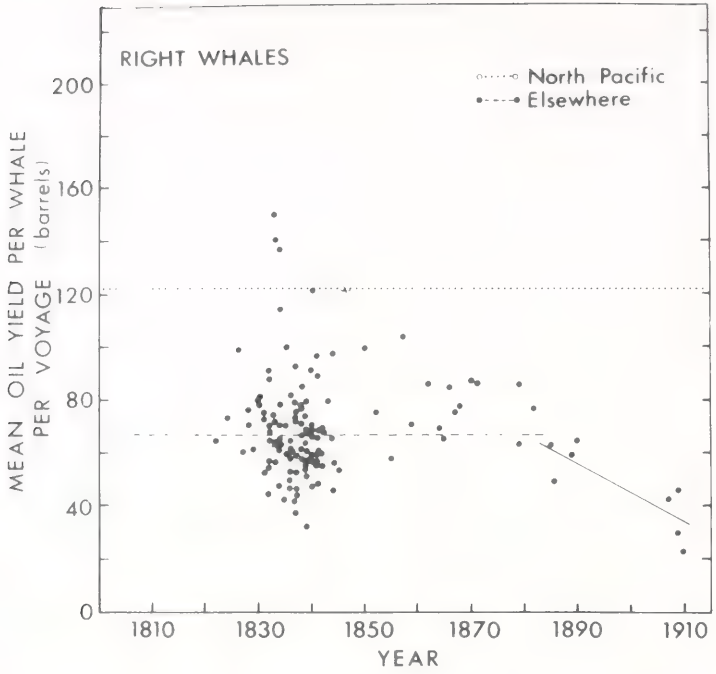

FIGURE 1.—Mean oil yield per whale for right whales landed on U.S. voyages from 1822 to 1910.

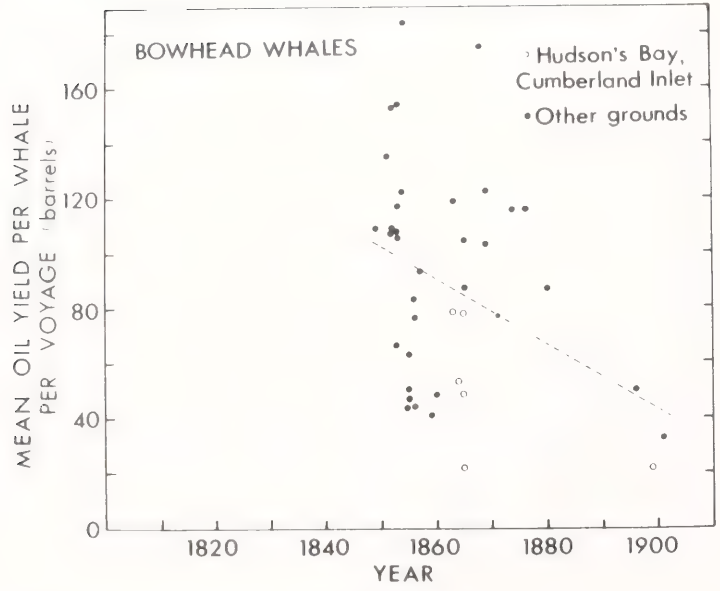

FIGURE 2.—Mean oil yield per whale for bowhead whales landed on U.S. voyages from 1849 to 1901.

where x = year of arrival (>1882) and
y = average oil yield (barrels).

This produces a decline from 63.7 barrels in 1883 to 34.2 barrels in 1910.

Prior to 1883 there was no significant trend with time ($b = 0.16 \pm 0.16$, $t = 1.01$, $P > 0.2$), so the average overall oil yield of 206,328/3,080 or 67 barrels (CV = 0.024) per whale has been used. Right whales in the South Atlantic were said to yield (when full grown) from 40 to 60 barrels of oil if male and 60 to 80 barrels if female, or about 60 barrels on average. Those in the South Pacific and Indian Oceans were said to be smaller, averaging 40 barrels if male and 60 barrels if female (Clark 1887a). Eleven right whales taken in the Indian Ocean averaged 59 barrels, with a maximum of 80 barrels (Wray and Martin 1983). In a sample of 29 right whales taken in the North Atlantic, Reeves and Mitchell (1986) found a range of oil yields from 6.5 to about 100 barrels with a mean of 58 to 59 barrels. These figures all agree fairly well with the calculated values used here: the decline in yield after 1883 may reflect market considerations and the relative value of oil and whalebone (see below).

Bowhead Whales

Oil yield data were available for 39 voyages on which 987 bowhead whales were taken; six voyages were to "Hudson's Bay" or "Cumberland Inlet" (Fig. 2). The latter voyages had generally lower oil yields (22 to 79 barrels) than the other grounds (32 to 184 barrels), possibly reflecting differences in distribution of size groups, or the effects of greater depletion. However, as no distinction was made in Townsend's (1935) tabulations between bowhead whales caught on different grounds, the data set has not been subdivided. Oil yields seemed to decline throughout the period of the fishery ($b = -1.19 \pm 0.48$, $t = 2.46$, $P < 0.02$), so for any particular year the mean oil yield has been calculated from the estimating equation:

$$y = 105.11 - 1.1892\,(x - 1848)$$

where x = year of arrival (>1848) and
y = average oil yield (barrels).

The slope of this regression is very sensitive to the three data points after 1890; their exclusion results in a much slower, nonsignificant rate of decline ($b = -0.58 \pm 0.73$, $t = 0.79$, $P > 0.20$). However, in view of the decreasing oil yields with time found by other workers and the economic incentives after 1880 that favored the collection of whalebone rather than whale oil (see below), the regression coefficient shown in Figure 2 has been retained.

This produces a decline from 103.9 barrels in 1849 to 31.4 barrels in 1910; yields before 1849 (for which no data exist) are taken as 103.9 barrels per whale.

According to Scammon (1874), bowhead whales could be classified into three types, yielding on average 200 barrels, 100 barrels, and 75 barrels of oil. Bowhead whales in the Davis Strait were said to average about 120 barrels (males 100, females 140), but had decreased in size "of late years". In the Okhotsk Sea, cows averaged about 130 barrels and the bulls about 90 barrels, but once again the whales had been much smaller "during recent years" (Clark 1887a). Oil yields for 333 whales from the Western Arctic stock listed by Bockstoce and Botkin (1983) averaged 112.4 barrels. These averages are all somewhat higher than the yield calculated here, but (with the exception of the last) they referred principally to the commencement of the fishery. Bockstoce and Botkin (1983) have also documented a decline in the size of bowhead whales taken over time, but the regression of barrels per whale per year has a somewhat smaller slope (−0.61 barrels per year) than in the present case: the mean yield declined from about 119 barrels in 1850 to about 70 barrels in 1900 (cf 43 in the present data). This difference may simply reflect a different measurement—Bockstoce and Botkin apparently only considered the yield of animals for which a barrel-estimate was made by the whaling vessel so that animals may have been excluded if no oil was rendered from them. The present analysis however considers all whales taken on a voyage (whether processed into oil and whalebone or not), so that it is not surprising that its figures are somewhat lower than for previous estimates. An oil yield as low as 49 barrels per whale was calculated for bowhead whales in Hudson Bay between 1860 and 1890 (Ross 1974).

Humpback Whales

Oil yield data were available for 29 cruises on which 1,137 humpback whales were taken (Fig. 3). There was no significant trend with time ($b = 0.31 \pm 0.19$, $t = 1.58$, $P > 0.10$), so the aver-

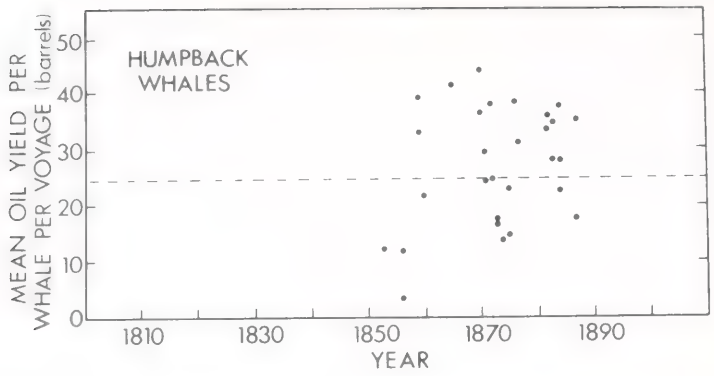

FIGURE 3.—Mean oil yield per whale for humpback whales landed on U.S. voyages from 1853 to 1887.

age overall oil yield of 27,797/1,137 or 24.4 barrels (CV = 0.110) per whale has been used throughout. According to Scammon (1874), humpback whales varied more in their production of oil than all other rorquals. Some individuals yielded only 8 or 10 barrels, whereas others gave up to 75 barrels; large females yielded on average 40 barrels. Mitchell and Reeves (1983) used an average of 25 barrels per whale, although individual whales yielded from 5 to 85 barrels each. The value calculated here is thus in reasonable agreement with previous estimates.

Gray Whales

There were no cruises in Townsend (1935) on which gray whales were the only baleen whale species taken, on which at least 10 animals were landed, and for which production figures were available in Starbuck (1878). Consequently the average production figure of 35 barrels per whale estimated by Henderson (1972) has been used throughout.

Average Yield of Whalebone Per Whale

Average yields of whalebone have been calculated essentially the same way as for oil. However, as Starbuck (1878) pointed out, in the earlier years (before about 1844/45), reports of the amount of bone taken were only occasional:

> Most of that commodity was imported prior to 1840 in New London and Sag Harbor ships, its value being so low that captains of vessels from many of the other ports did not care to be encumbered with it. For this reason a large amount of bone was brought home which it is impossible to properly accredit.

Figures for whalebone landings were listed for 94 to 95% of the voyages on which bowhead or North Pacific right whales were taken, but for only 30 and 24% of the voyages taking other right and humpback whales respectively. Two alternative (and probably extreme) assumptions can therefore be made: A) that only those vessels listed as landing whalebone actually did so, or B) that all vessels taking baleen whales retained the whalebone to the same extent as those for which whalebone production was reported. Average whalebone yields per whale (and trends therein) have been calculated here under both assumptions A and B (Figs. 4-7).

Right Whales

Of the 17 voyages on which 10 or more right whales were taken in the North Pacific, whalebone production was reported for 16 (Fig. 4). There was no significant trend in bone yield per whale in all 17 voyages ($b = -6.36 \pm 13.98$, $t = 0.46$, $P > 0.6$) or in the 16 for which bone production was declared ($b = -12.84 \pm 12.14$, $t = 1.06$, $P > 0.3$). Consequently overall mean yields of 384,134/341 or 1,126 lb (CV = 0.098) whalebone (assumption A) and 384,134/323 or 1,189 lb (CV = 0.082) whalebone (assumption B) have been used. According to Clark (1887a), whalebone yield in North Pacific right whales averaged about 1,000 lb per 100 barrels (equivalent to a yield of 1,250 lb for an average whale), while Scammon (1874) gave a range of 1,000 to 1,500 lb.

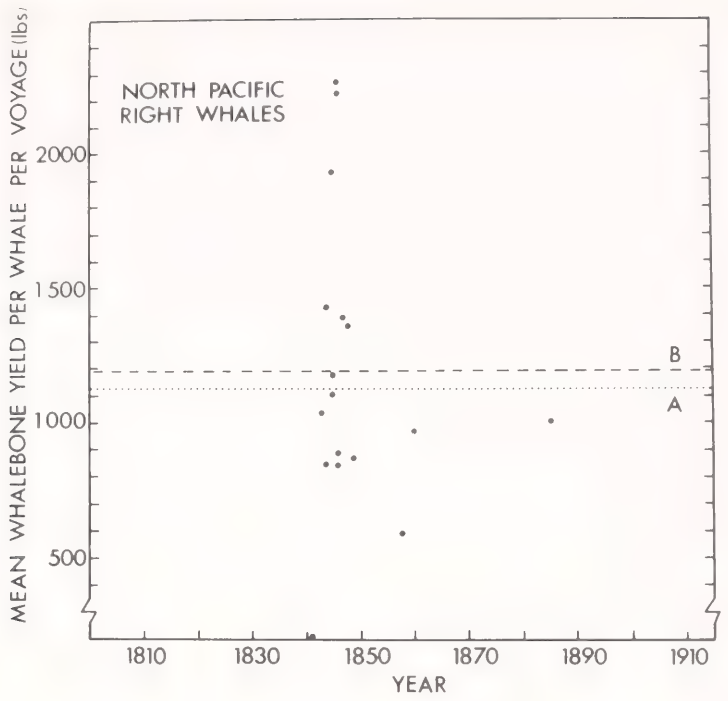

FIGURE 4.—Mean whalebone yield per whale for North Pacific right whales landed on U.S. voyages from 1841 to 1885 (A = assuming only those vessels listed as landing whalebone actually did so, B = assuming all vessels taking whalebone whales retained the whalebone to the same extent as those for which whalebone production was reported).

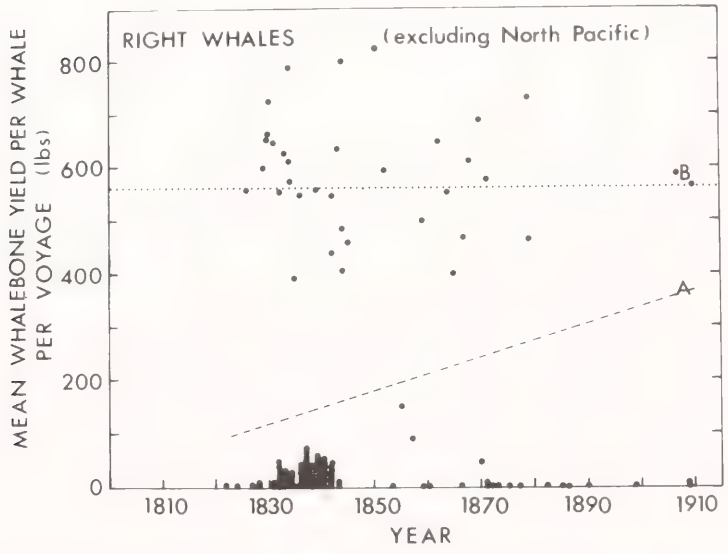

FIGURE 5.—Mean whalebone yield per whale for right whales landed on U.S. voyages (other than in the North Pacific) from 1822 to 1910 (A = assumption A, B = assumption B).

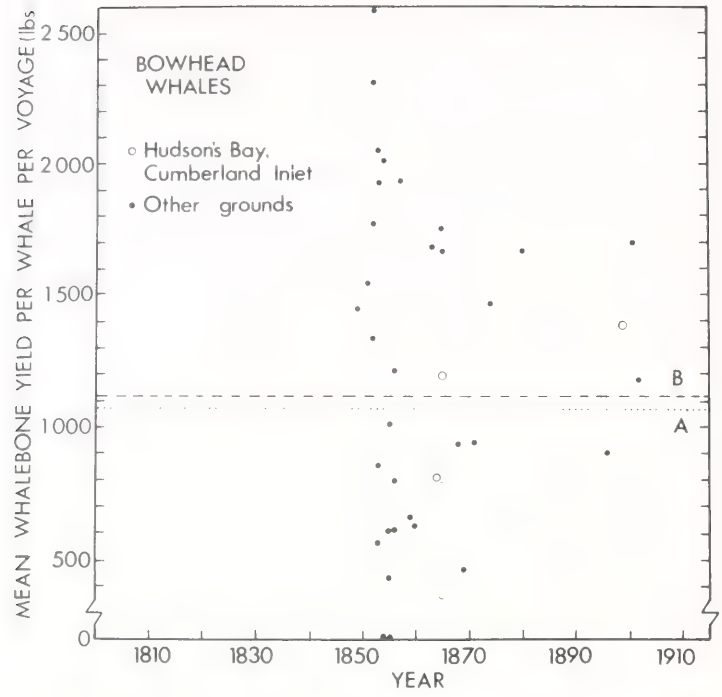

FIGURE 6.—Mean whalebone yield per whale for bowhead whales landed on U.S. voyages from 1849 to 1902 (A = assumption A, B = assumption B).

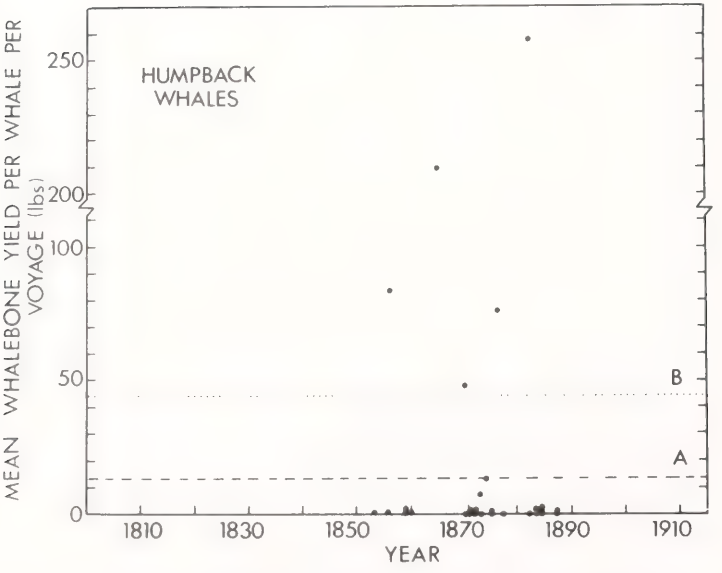

FIGURE 7.—Mean whalebone yield per whale for humpback whales landed on U.S. voyages from 1853 to 1887 (A = assumption A, B = assumption B).

Present calculations are therefore close to these estimates.

Of the 127 voyages taking right whales on grounds other than the North Pacific, bone yields were available for only 37 (Fig. 5). For all 127 cruises there was a significant trend in mean yield with time ($t = 2.40$, $P < 0.02$), so annual values under assumption A were calculated from the least squares estimating equation:

$$y = 92.51 + 3.11\ (x - 1821)$$

where x = year of arrival (>1821) and
y = average whalebone yield (lbs).

This equation produces a yield of 96 lb per whale in 1822 and a yield of 370 lb per whale in 1910: yields before 1822 (for which no data exist) are taken as 96 lb per whale.

For the 37 cruises where bone production was declared, there was no significant trend in average yields with time ($b = -0.67 \pm 1.26$, $t = 0.53$, $P > 0.6$), so the overall mean yield of 497,840/884 or 563 lb (CV = 0.043) of bone per whale has been used under assumption B. This agrees well with a calculated mean of 629 lb and adult range of 250 to 330 kg (550 to 726 lb) for right whales from South Africa (Best 1970) and the North Atlantic (Collett 1909), respectively. Clark (1887a) stated that right whales in the South Atlantic yielded on average about 300 lb of bone per 100 barrels of oil in the male and 400 to 600 lb per 100 barrels in the female (equivalent to an actual yield of about 180 lb per whale in the male and 240 to 360 lb in the female). Although he claimed that right whales in the Indian Ocean were smaller than those in the South Atlantic, average whalebone yields are given as 240 lb for males and 360 lb for females. It is not clear why Clark's figures are somewhat lower than the others quoted here.

Bowhead Whales

Of the 39 voyages taking bowhead whales that were analyzed, 37 included reference to landings of whalebone (Fig. 6). There was no significant trend in the mean yield of whalebone per whale, either under assumption A ($b = 0.03 \pm 7.19$, $t = 0.005$, $P > 0.9$) or B ($b = -2.87 \pm 6.66$, $t = 0.4305$, $P > 0.6$). Overall mean yields can therefore be calculated as 1,060,911/993 = 1,068 lb (CV = 0.098) per whale (assumption A) or 1,060,911/949 = 1,118 lb (CV = 0.095) per whale (assumption B). According to Clark (1887a), the yield of bone in bowhead whales from the Atlantic-Arctic grounds averaged about 1,300 lb to 100 barrels of oil (or about 1,560 lb per whale), whereas in the Okhotsk Sea the yield was about 1,500 lb to 100 barrels of oil (or about 1,650 lb per whale). In both areas, however, Clark commented that whales found there "during recent years" were much smaller than those taken at the beginning of the fishery; the values given above referred essentially to the start of the fishery. Ross (1974) calculated the average yield for a bowhead whale from the Hudson Bay stock as 1,065 lb, later revised to 916 lb (Ross 1979). For whales from the Davis Strait stock, the average yield was calculated as 1,392 lb (Ross 1979). Present estimates are therefore within the range of those given previously.

Humpback Whales

Of the 29 voyages taking humpback whales that were analyzed, only 7 had associated whalebone production (Fig. 7). There was no significant trend in the mean yield of whalebone per whale, either under assumption A ($b = -0.21 \pm 1.20$, $t = 0.17$, $P > 0.8$) or B ($b = 1.95 \pm 5.12$, $t = 0.38$, $P > 0.7$), so the relevant overall means have been used, i.e., 15,116/1,137 = 13 lb (CV = 0.416) under assumption A and 15,116/345 = 44 lb (CV = 0.652) under assumption B. Scammon (1874) stated that humpback baleen was of inferior quality, but could be collected at a rate of about 400 lb per 100 barrels of oil; this would be equivalent in current calculations to a yield of 98 lb whalebone per whale. Mitchell and Reeves (1983) confirmed that baleen from humpback whales was generally considered of poor quality, but pointed out that it was occasionally marketed.

Gray Whales

There were no voyages available on which 10 or more gray whales were taken and for which whalebone production was declared. According to Henderson (1972:84):

> Unlike the valuable baleen of the right and bowhead whales, whalebone from the gray never became an important part of the catch . . . little bone was recorded in the cargos of the gray whaling vessels. The few recorded cargos of gray whalebone to arrive in San Francisco and

San Diego did not appear until gray whaling was in decline and the price of right and bowhead whalebone had risen considerably after the mid 1860s.

Rather than adopting an arbitrary value for the average whalebone yield of gray whales, it has been taken as zero. This means that estimates of the size of the catch of other species using whalebone production may be correspondingly overestimated by an unknown but probably small amount. However, as whalebone production is used only to estimate the landed catch from 1880 onwards (see below), and there are no gray whales in the logbook sample after this date, the practical effect of this assumption is minimal.

Estimates of Total Landed Catch of Whalebone Whales

Figures for the importation of whale products into the United States have been based on table J of Starbuck (1878), supplemented by data in Hegarty (1959). As pointed out by Starbuck, it would appear from a comparison of imports and exports from 1804 to 1817 that much oil and bone must have been imported which was not credited to any port, and thus did not appear in table J. After 1817 exports as listed by Starbuck totalled 0.373 of imports for whale oil and 0.697 for whalebone. It was presumably these figures that led Starbuck (1878) to propose that exportation of whale oil and bone for 1804 to 1817 represented one-third and two-thirds respectively of the importation, and I have followed his proposal in adjusting the figures for 1804 to 1817 upwards on a prorata basis. The validity of this assumption is of course unknown.

Inspection of table K in Starbuck (1878) also shows that importation figures for whalebone from 1838 to 1842 were "estimated" or "assumed", apparently at a rate of 10 lb of whalebone per barrel of oil, and may not therefore be very reliable. The data, summed by five yearly periods, are shown in Table 2.

In order to estimate the total landed catch for any 5-yr period, the catch of each species given in Table 1 has been multiplied by its mean yield of oil or whalebone (corrected for the relevant year of catch, if necessary, using the median year in any 5-yr period) and the resulting production figures summed. Comparison of this total with that in Table 2 for the same period then provides a scaling factor by which the catches in Table 1 have to be multiplied to obtain the total landed catch for that period. These scaling factors are shown in Table 2.

In two of the three data sets (those for oil and whalebone factor A), there was a tendency for the scaling factors to be particularly high at the beginning of the time series, indicating that logbook coverage (and hence the reliability of extrapolations) was poor in the earlier years. The great differences between the two scaling factors for whalebone before about 1845 suggests either that a lot of whalebone was not being collected from the whales taken, or that it was not possible to allocate imports of it to a particular port or vessel (Starbuck 1878). The low ratio of whalebone to whale oil imported from 1805 to 1834 (Table 2) would indicate that the former was the more likely. Given the unreliability of import figures for whalebone from 1804 to 1817 and between 1838 and 1842, this suggests that oil production figures would be a more appropriate measure of the landed catch before about 1845.

All three factors converge closely from 1855 to 1879, presumably indicating that full utilization was being made of both whalebone and whale oil. During this period the ratio of whalebone to whale oil imported ranged from 7.7 to 11.0, with a mean of 9.1 lb to a barrel of oil (Table 2).

After 1880 the factors tend to diverge again, but this time the divergence is mainly between

TABLE 2.—Five-year compilation of imports of whalebone and whale oil into the United States (from Starbuck 1878 and Hegarty 1959).

Period	Total U.S. imports		Ratio: Bone oil	Scaling factors[1]		
	Whale oil (barrels)	Whalebone (lb)		Oil	Bone A	Bone B
1805–09	285,969	360,981	1.3	99.3	87.7	14.9
1810–14	96,759	151,921	1 6	—	—	—
1815–19	130,666	179,793	1.4	58.2	23.2	9.1
1820–24	246,793	429,447	1.7	45.5	55.4	9.4
1825–29	245,777	1,039,134	4.2	13.6	34.7	6.9
1830–34	680,729	1,846,907	2.7	9.4	13.4	3.0
1835–39	917,064	7,947,069	8 7	8.4	34.8	8 8
1840–44	1,032,080	10,159,715	9.8	9.1	19.0	10.2
1845–49	1,324,305	14,073,773	10.6	7.4	9.9	8.3
1850–54	1,193,253	17,143,100	14.4	8.3	12.3	11 2
1855–59	985,480	10,854,100	11 0	5.9	6.6	6.0
1860–64	509,037	4,388,800	8.6	5.0	4.9	4.3
1865–69	390,415	4,045,575	10.4	4.1	4.4	3.9
1870–74	256,714	2,054,769	8.0	3.9	3.8	3.3
1875–79	152,907	1,176,690	7.7	6.5	7.8	6.2
1880–84	138,654	1,785,354	12.9	4.6	10.7	8.1
1885–89	134,438	1,989,176	14.8	5.9	10.7	9.4
1890–94	62,614	1,667,478	26.6	7.6	15.0	12.9
1895–99	21,531	1,067,130	49.6	2.0	5.0	4.7
1900–04	17,175	614,830	35.8	4.0	6.8	6.3
1905–09	15,710	460,100	29.3	3.5	6.8	5.3

[1]Rounded to one decimal place.

the oil factor and both whalebone factors. This is accompanied by a marked increase in the ratio of whalebone to whale oil imported, to a peak of 49.6 lb to a barrel of oil from 1895 to 1899 (Table 2). It is assumed that over this period whalebone was collected in preference to whale oil, as described by Ross (1974) for bowhead whales:

> . . . with a dramatic rise in the price of whalebone the oil diminished to less than 20% of the value of a whale after 1890 . . . . As a result whaling masters intensified the search for bone; . . . the crews simply stripped away the baleen, which was readily transportable, and left the rest of the carcass, including the bulky blubber, to rot. Oil returns, therefore, do not accurately reflect the number of whales killed in the late decades of whaling.

It is apparent that after 1880, whalebone production would be a more accurate measure of the total landed catch.

The economic basis for these shifts in interest is clearly shown by the average prices of whale oil and whalebone imported into the United States each year from 1804 to 1909 (Starbuck 1878; Hegarty 1959). These have been used to calculate the relative contribution of whalebone to the total value of a right whale, assuming a ratio at maximum utilization of 10 lb of bone to a barrel (= 31.5 gal) of oil per whale (Table 3). Whalebone made a relatively minor contribution to the value of a whale (<20%) up to 1839, ranged from 20 to 34% between 1840 and 1874, but increased rapidly in value thereafter to a peak of 80.8% in 1905-09.

TABLE 3.—Prices paid for whale products imported into the United States and the relative value of whalebone from a right whale.

Period	Average price (US$)		% Contribution whalebone in total value of adult right whale
	Whale oil (per gal)	Whalebone (per lb)	
1805–1809	0.48	0.08	5.0
1810–1814	0.64	0.09	4.2
1815–1819	0.59	0.11	5.6
1820–1824	0.32	0.12	10.6
1825–1829	0.29	0.20	18.0
1830–1834	0.29	0.17	15.7
1835–1839	0.37	0.21	15.3
1840–1844	0.33	0.28	21.2
1845–1849	0.35	0.29	20.8
1850–1854	0.44	0.38	21.5
1855–1859	0.65	0.76	27.1
1860–1864	0.75	1.14	32.5
1865–1869	1.05	1.30	28.2
1870–1874	0.64	1.02	33.6
1875–1879	0.50	2.09	57.0
1880–1884	0.53	2.35	58.5
1885–1889	0.37	2.96	71.7
1890–1894	0.41	4.20	76.5
1895–1899	0.34	3.10	74.3
1900–1904	0.37	3.88	76.9
1905–1909	0.33	4.38	80.8
1910–1914	0.37	0.63	35.1

To conclude, oil production is considered the more accurate measure of the landed catch from 1804 to 1879, but whalebone production thereafter. With the high value of whalebone after 1879 (comprising more than half the total value of the whale), it is likely that it would be utilized whenever possible. Hence scaling factor B would be the more appropriate to use.

Using these factors, the total landed catch from the data tabulated by Townsend (1935) for American vessels only between 1804 and 1909 is estimated as 125,883 whales, comprising 30,313 bowhead, 74,693 right, 18,212 humpback, and 2,665 gray whales (Table 4). Of the right whales caught, 182 (0.2%) were taken in the North Atlantic, 15,374 (20.6%) in the North Pacific, 32,191 (43.1%) in the South Atlantic, 14,699 (19.7%) in the South Pacific, and 12,247 (16.4%) in the Indian Ocean.

ESTIMATES BASED ON CATCH PER VOYAGE

The use of production figures to estimate catches masks certain fundamental problems. According to R. C. Kugler (in litt. 6 March 1985), neither Starbuck nor Hegarty apparently made much effort to report a vessel's total take of oil. They relied primarily on newspapers, especially the Whalemen's Shipping List after it began publication in 1843. These reports, however, seldom gave more than the amount of oil on board at the time of the vessel's arrival. Only sporadically and inconsistently was shipped oil added in. This factor would mean that the mean oil yields per whale calculated here would be underestimated, and the total number of whales landed correspondingly overestimated. Nevertheless, the mean oil yields derived in this paper agreed reasonably well with contemporary opinion on how much a particular species should yield.

A further problem with the use of whale oil production is that the term "whale oil" was used to designate not only that from right and other species of whalebone whale, but also elephant seal and walrus oil. At certain periods the amounts landed of the latter were not negligible (Bockstoce and Botkin 1982; Busch 1985; Kugler in litt. 6 March 1985). However, it is not clear how much and in which direction this factor would affect the present analysis, depending on whether

TABLE 4.—Numbers of baleen whales landed by U.S. whalers, 1805–1909, based on oil production up to 1879 and whalebone production thereafter.

Period (arrival)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl.	Pac.	Ind.			
1805–09	—	—	—	4,268	—	—	—	—	4,268
1810–14	—	—	—	—	—	—	—	—	—
1815–19	291	—	—	175	1,281	—	116	—	1,863
1820–24	—	—	—	3,683	—	—	—	—	3,683
1825–29	—	—	—	3,663	—	—	14	—	3,677
1830–34	—	—	—	8,804	665	674	47	—	10,190
1835–39	—	—	—	6,394	2,991	4,008	807	—	14,200
1840–44	—	—	2,957	484	4,709	4,608	602	—	13,360
1845–49	669	—	8,001	404	2,567	949	654	—	13,244
1850–54	9,103	—	1,364	728	281	397	694	50	12,617
1855–59	7,273	6	1,381	311	423	488	1,422	382	11,686
1860–64	3,250	45	585	545	520	240	965	1,025	7,175
1865–69	2,956	8	441	445	103	177	511	886	5,527
1870–74	1,815	—	58	173	69	177	2,983	270	5,545
1875–79	677	39	85	352	7	85	2,475	52	3,772
1880–84	958	32	8	620	209	—	4,985	—	6,812
1885–89	711	47	356	496	674	28	1,600	—	3,912
1890–94	1,108	—	39	490	168	—	284	—	2,089
1895–99	860	5	56	33	—	28	47	—	1,029
1900–04	468	—	38	70	—	13	6	—	595
1905–09	174	—	5	53	32	375	—	—	639
Total	30,313	182	15,374	32,191	14,699	12,247	18,212	2,665	125,883

the whale oil production of the voyages listed by Townsend was diluted to a greater or lesser extent with seal and other oil than the total production.

The catch-per-voyage analysis attempts to avoid the problems created by the incomplete reporting of the products of a voyage, and (at least partially) those arising from the dilution of whale oil with seal, walrus, and other oils.

In order to make some further correction for voyages that were entirely devoted to sealing, all voyages recorded as returning only elephant oil, or as "skinning voyages", or voyages labelled as sealing by Starbuck (1878) and Hegarty (1959) have been excluded. In addition, all voyages from the Connecticut ports of New London, Stonington, or Mystic that were recorded as being bound for S. Shetlands, Desolation, Falklands, Hurds Island, or Crozettes and that returned with whale oil but no whalebone have been omitted on the grounds that these were probably sealing voyages. This has resulted in a total omission of 141 voyages between 1804 and 1921.

Obviously this figure does not include all voyages on which seal oil was taken, as many seals were taken on combination sealing/whaling voyages. Between 1840 and 1890, an average 25% of "whaling" vessels leaving New London are said to have visited Desolation or Heard Island for elephant seals (Busch 1985), but of 110 voyages departing to these islands from New London during this period, 45 were reported as bringing back sperm oil and/or whalebone as well as "whale" oil (Starbuck 1878; Hegarty 1959).

Starbuck (1878) and Hegarty (1959) also listed a number of mixed voyages from other ports in which small amounts of whale oil were landed but no whalebone. While some of these might represent voyages on which whales with inferior whalebone (such as humpback or gray whales) were taken, other such small consignments of whale oil might have originated from seals or from "blackfish" (pilot whales *Globicephala* spp.). Pilot whales were sometimes taken by whalemen to supplement their cargoes, the oil being rated as common whale oil. Clark (1887b) listed 36 voyages on which from 2 to 200 barrels of blackfish oil was brought home, 33 (91.7%) of them bringing back 100 barrels or less. To investigate this further, mixed voyages on which 100 barrels or less of whale oil but no whalebone were landed (from Starbuck and Hegarty) were compared with the catch composition of the same voyages as given by Townsend (1935). Of 153 such voyages, baleen whales were reported as being taken on 55 (35.9%) voyages, with the proportion approaching 100% as the amount of whale oil approached 100 barrels (Table 5). Consequently for each 5-yr time period the number of mixed voyages reporting 100 barrels or less of whale oil but no whalebone was adjusted by the proportion of such voyages in Townsend's sample that were reported as taking

TABLE 5.—Proportion of mixed voyages by U.S. whalers landing small consignments of whale oil (but no whalebone) on which whalebone whales were taken.

Amount of whale oil reported (barrels)	Number of mixed voyages examined	Proportion of mixed voyages on which whalebone whales taken
1–10	53	0.113
11–20	19	0.263
21–30	18	0.444
31–40	14	0.500
41–50	11	0.364
51–60	10	0.300
61–70	12	0.750
71–80	8	0.750
81–90	2	1.000
91–100	6	0.833

baleen whales during the same period. This resulted in an effective conversion of 812 mixed voyages between 1805 and 1910 to sperm whaling voyages.

Because Starbuck (1878) and Hegarty (1959) listed voyages by the year of departure, the data in the catch-per-voyage analysis has been compiled against year of departure rather than (as was done for the production-based analysis) by year of arrival. The numbers of sperm, mixed, and whalebone voyages in Townsend's sample for each 5-yr period are given in Table 6, together with the scaling factors A1 and A2 for mixed and whalebone whalers respectively. The latter represent the ratio of the number of voyages of each type in the Townsend sample to the number of similar voyages in Starbuck/Hegarty for that period, after correction (as described above) for voyages believed to be sealing rather than whaling. These scaling factors are then applied to the total numbers of whales landed in the Townsend sample for that period and voyage-type, and the results for each voyage-type added to give the total number of each species for that period.

This analysis provides an estimate of the landed catch of whalebone whales from American vessels between 1805 and 1914 as 117,308, comprised of 29,788 bowhead, 70,343 right, 14,164 humpback, and 3,013 gray whales (Table 7). Of the right whales, 186 (0.3%) were taken in the North Atlantic, 14,480 (20.6%) in the North Pacific, 28,532 (40.6%) in the South Atlantic, 14,652 (20.8%) in the South Pacific, and 12,493 (17.8%) in the Indian Ocean.

Table 6.—Breakdown of Townsend's (1935) sample into voyage-type, with scaling factors (A1, A2) derived from numbers of such voyages in Starbuck (1878) and Hegarty (1959).

Period (departure)	Type of voyage: Sperm	Mixed		Whalebone		
	n	*n*	A1	*n*	A2	Total
1805–09	2	1	8.00	1	51.00	4
1810–14	1	0	—	0	—	1
1815–19	3	1	89.00	2	49.50	6
1820–24	6	3	23.67	1	117.00	10
1825–29	10	12	8.92	8	13.38	30
1830–34	29	47	6.00	11	18.09	87
1835–39	54	75	8.28	9	12.33	138
1840–44	56	88	8.64	4	28.75	148
1845–49	53	93	6.25	8	9.88	154
1850–54	51	102	5.74	9	16.56	162
1855–59	52	101	5.29	11	11.82	164
1860–64	49	54	4.76	16	3.06	119
1865–69	55	83	4.02	13	5.46	151
1870–74	30	31	4.77	4	6.75	65
1875–79	44	48	3.67	7	6.14	99
1880–84	29	28	4.32	11	11.91	68
1885–89	17	22	2.91	14	13.79	53
1890–94	18	16	2.56	8	18.50	42
1895–99	7	11	3.27	10	5.90	28
1900–04	22	9	2.67	10	4.70	41
1905–09	19	10	1.60	5	5.80	34
1910–14	11	2	2.50	3	2.67	16
Total	618	837		165		1,620

DISCUSSION

The two methods used give somewhat similar results, estimates of the landed catch differing by <10% in all cases except for South Atlantic right whales and humpback whales (where the production-based estimates exceeded the catch per voyage estimates by 13 and 29% respectively) and gray whales (where the catch per voyage estimate exceeded the production estimate by 13%).

Nevertheless, both sets of estimates are essentially derived from the same basic data (Townsend's sample), and a more fundamental problem with both analyses is how representative this sample was of the contemporary Yankee fishery. The 1,651 voyages examined by Townsend are equivalent to only 12% of the estimated total number of voyages made by American pelagic whalers (Sherman 1965), but the scaling factors in Tables 2 and 6 indicate that the coverage of voyages in some periods (particularly prior to 1830) was much less than this. Unless the logbook sample is truly random with respect to the species and numbers of whales taken, any simple reconstruction of the total catch therefrom is likely to be inaccurate.

The catch per voyage analysis included some stratification of the Townsend sample, so that extrapolations to the total fleet might be more representative. To this extent, therefore, the catch per voyage method might seem the more reliable,

TABLE 7.—Numbers of whalebone whales landed by U.S. whalers, 1805–1914, as calculated from the catch per voyage.

Period (departure)	Bowhead	Northern right		Southern right			Humpback	Gray	Total
		Atl.	Pac.	Atl	Pac	Ind			
1805–09	—	—	—	1,849		—	—	—	1,849
1810–14	—	—			—	—	—	—	—
1815–19	248	—	—	149	1,958	—	178	—	2,533
1820–24	—	—	—	4,468	—	—	—	—	4,468
1825–29	—	—	—	3,617	535	—	63	—	4,215
1830–34	—	—	—	8,902	390	600	384	—	10,276
1835–39	—	—	149	5,662	5,190	5,561	285	—	16,847
1840–44	—	—	5,728	598	3,542	3,939	657	—	14,464
1845–49	2,148	—	5,578	515	1,485	421	669	—	10,816
1850–54	10,260	6	951	511	161	775	565	281	13,510
1855–59	5,454	48	1,221	429	579	501	2,317	1,279	11,828
1860–64	2,583	—	152	516	280	96	447	665	4,739
1865–69	3,215	11	434	354	105	342	2,153	755	7,369
1870–74	744	—	52	81	14	29	2,561	33	3,514
1875–79	417	40	16	400	95	40	1,801	—	2,809
1880–84	604	9	48	216	186	—	1,881	—	2,944
1885–89	729	69	90	113	122	9	134	—	1,266
1890–94	2,098	—	26	44	—	—	59	—	2,227
1895–99	715	3	16	23	—	26	10	—	793
1900–04	353	—	19	27	—	—	—	—	399
1905–09	180	—	—	40	10	154	—	—	384
1910–14	40	—	—	18	—	—	—	—	58
Total	29,788	186	14,480	28,532	14,652	12,493	14,164	3,013	117,308

but other problems (allowance for sealing voyages, correct allocation of incomplete voyages) may not have been adequately solved. Furthermore, even the stratification by voyage-type may have been insufficient to correctly portray the species composition of the total fleet; an alternative procedure might be to stratify by home port, but this would probably involve too fine a stratification for the size of the sample available.

A further problem identified with the Townsend sample is that there may be occasional misidentification or omission of catches (see Bockstoce and Botkin 1983). There is no indication of the extent of this problem (which would require checking Townsend's tabulations against the original journals), but it means that the accuracy of the extrapolations made in this paper may be adversely affected to an unknown degree.

Some independent estimates of the landed catch of various stocks have been made. Henderson (1972) estimated that 4,958-5,058 Californian gray whales were taken by pelagic whalers between 1846 and 1874, whereas calculations from the Townsend sample are that 2,665 to 3,013 gray whales were taken over the period 1850 to 1879. Henderson's estimate, however, includes the catches of non-U.S. vessels. From data in Henderson's table II it can be calculated that 64.9% of the 21,135 barrels of oil from Scammon's Lagoon between 1858 and 1873 were taken by U.S.-registered vessels. If this proportion is applied to the total catch, it means that U.S. pelagic whalers may have accounted for a landed catch of 3,218 to 3,283 gray whales. On this basis, calculations from the Townsend sample may be about 6 to 19% too low.

Bockstoce and Botkin (1983) calculated that 16,600 bowhead whales were taken from the Western Arctic population by the pelagic whaling industry between 1849 and 1914; this apparently included catches by non-U.S. vessels. Henderson has also estimated that the total catch of bowhead whales from the Okhotsk Sea stock between 1847 and 1867 was about 15,200 animals, with another 92 known to have been taken between 1867 and 1896 (Kugler 1984). About 90% of the voyages to the Okhotsk Sea between 1847 and 1867 were made by American whaleships, which if considered applicable to the catch would mean that they took about 13,760 bowhead whales from 1847 to 1896. Ross (1979) has estimated the catch of bowhead whales by American whalers in the Davis Strait from 1847 to 1891 as 413, and that in Hudson Bay from 1860 to 1912 as 532 animals; his figure for the Beaufort Sea of 794 bowhead whales between 1889 and 1908 is assumed to be included in Bockstoce and Botkin's calculations for the entire Western Arctic. Combining the data from Ross (1979), Bockstoce and Botkin (1983), and Kugler (1984) indicates a total bowhead

catch of 31,305 animals (some of which may have been taken by non-U.S. vessels). This is 3 to 5% higher than the total estimate of 29,788 to 30,313 bowhead whales from the Townsend sample.

Reeves and Mitchell (1986) have attempted to reconstruct the American pelagic catch of right whales in the North Atlantic during the nineteenth century. They document at least 116 right whales that were killed and processed by pelagic whales between 1855 and 1897. The present analysis indicates a total landed catch by U.S. whalers of 182 to 186 right whales over the same period.

These comparisons suggest that, apart from gray whales, the estimates of landed catch obtained in this paper are not unduly biased. They are, however, clearly only first approximations. A much more detailed approach, including examination of primary source material, is required before a more reliable assessment of the American catch of right whales can be made. In particular, there needs to be more adequate sampling of logbooks prior to 1830.

It should also be stressed that the figures produced here are estimates of the landed catch; further work is needed to determine the numbers of animals that were struck and lost, and the proportion of these that might have died, before an estimate of the total kill made by the American fishery can be made. Such research, requiring consultation of primary sources, is outside the scope of this paper. Nevertheless, a significant proportion of the landed catch of some species apparently consisted of whales found dead. In the Townsend abstracts examined here, there were records of 246 baleen whales processed that were found dead: 127 bowheads (6.3% of the landed catch), 103 right whales (2.9% of the landed catch), 5 humpback whales (0.4% of the landed catch), and 11 gray whales (or 4.4% of the landed catch). These figures might be underestimates if (as seems likely) not all the whales found dead were recorded as such in the logbooks or logbook abstracts. Most of these whales probably died as a result of whaling-related injuries. If so, this fact should be borne in mind when corrections are applied to the landed catch to account for whales struck and lost that subsequently died.

With no correction for animals dying after being struck and lost, the estimated number of right whales taken between 1805 and 1874 as calculated in this paper, 68,484 to 70,250 (of which 79% were southern right whales), is about one third of Starbuck's original estimate for the same period. This compares with an estimated total catch by French pelagic whalers between 1817 and 1868 of 11,000 right and bowhead whales (Du Pasquier 1986). Comparable figures for the British take are not yet available.

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ESTIMATING DENSITY OF DOLPHIN SCHOOLS IN THE EASTERN TROPICAL PACIFIC OCEAN BY LINE TRANSECT METHODS

RENNIE S. HOLT[1]

ABSTRACT

Data were collected from aerial and research ship surveys to estimate density of dolphin schools in the eastern tropical Pacific using line transect (LT) theory. The surveys were conducted from 1977 through 1983. Several assumptions of LT theory were investigated for both aerial and ship data. Factors were developed to alleviate effects of suspected violations of the assumptions. I estimated densities from data stratified into an inshore area surveyed by planes and an offshore area surveyed by ships. The density estimate for the inshore area was 4.18 schools/1,000 km^2 and 2.04 for the offshore area. For the entire area, the density estimate was 2.71 schools/1,000 km^2. Adjustments for possible biases owing to adverse sea state and sun glare conditions increased the inshore estimate by 8% and the total area estimate by 4%.

The National Marine Fisheries Service (NMFS) is responsible for assessing the status of those dolphin stocks taken incidentally by tuna purse seiners in the eastern tropical Pacific (ETP) Ocean. Techniques used to assess these stocks (Smith 1979[2]) require estimates of school density, so density estimates were made in 1975 (Smith 1975[3]) and in 1979 (Holt and Powers 1982). Since 1979, NMFS has collected additional information to test the assumptions of its statistical methods and to further survey the areas inhabited by the dolphins. In this paper, I present analyses of data collected from 1977 through 1983 to determine density estimates of dolphin schools in the ETP. In addition, I investigate several factors which may bias the estimates.

To obtain estimates of density of dolphins (individuals) it is further necessary to consider school size, the proportions of various species in mixed schools, and areas inhabited by the various stocks. Estimation of these factors is complex; they are to be dealt with elsewhere and are not addressed in this paper.

MATERIAL AND METHODS

Surveys

Data used to calculate the density of dolphin schools were collected during several years. Aerial surveys were conducted in 1977 and 1979 (Fig. 1), and nine research ship cruises were made during 1977, 1979, 1980, 1982, and 1983 (Fig. 1). Most surveys were conducted between January and early April; one of the 1977 ship cruises was made in October and the two 1980 cruises were made from May through August.

A two-engine PBY amphibious patrol bomber was used in the 1977 aerial survey (SWFC 1978[4]), and a four-engine PBY bomber was used in the 1979 aerial survey (Jackson 1980[5]). Operating and viewing conditions aboard the two aircrafts were similar. Both planes cruised at 148-240 km/hour (80-130 kn) and had bubble-shaped waist windows. The PBY used in 1977 had a flat bow window which was shaped like an isosceles trapezoid. The 1979 PBY had a round bubble-shaped bow window. The round bubble window allowed

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Smith, T. 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979). Southwest Fish. Cent. Adm. Rep. No. LJ-79-41, La Jolla, CA, 120 p.

[3]Smith, T. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Southwest Fish. Cent. Adm. Rep. No. LJ-75-65, La Jolla, CA, 88 p.

[4]SWFC (Southwest Fisheries Center). 1978. Aerial survey trip report, January-June 1977. Southwest Fish. Cent. Adm. Rep. No. LJ-78-01, 73 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[5]Jackson, T. 1980. Report: Porpoise population aerial survey of the eastern tropical Pacific Ocean, January 22-April 25, 1979. Southwest Fish. Cent. Adm. Rep. No. LJ-80-01, 74 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

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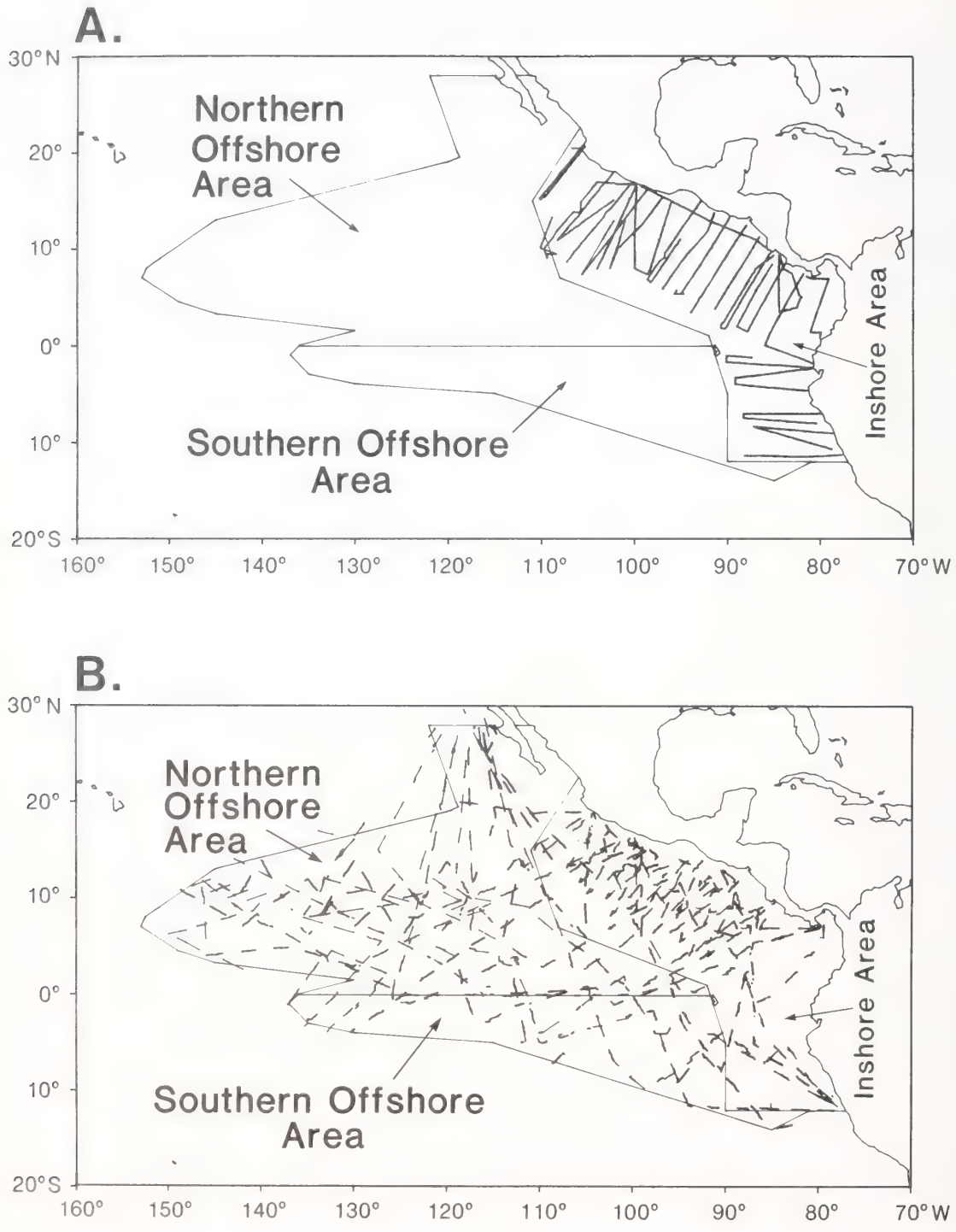

FIGURE 1.—Tracklines for 1977 and 1979 aerial (A) and combined 1977, 1979, 1980, 1982, and 1983 ship (B) surveys.

better lateral viewing, but both provided unobstructed forward and downward views.

Two research vessels were used to collect the shipboard data. The NOAA ship *David Starr Jordan* was used during all years and the NOAA ship *Townsend Cromwell* joined it in 1977, 1979, and 1980. Both vessels were similar in length and cruising ability. Binoculars used to locate animals were mounted approximately 10.7 m above the sea on the *Jordan* but were only 6.1 m above the sea on the *Cromwell*. In addition, observers aboard the *Jordan* used 20× binoculars during the 1977 surveys and 25× glasses on the rest of the surveys; observers aboard the *Cromwell* used only 20× glasses during their surveys. Consequently, viewing conditions were generally much better on the *Jordan*.

Study Area

Survey efforts traversed the combined range of ETP dolphin stocks defined by Au et al. (1979)[6]. The range was partitioned into "inshore" and "offshore" areas (Fig. 1). Airplanes were used to survey the inshore area, and ship surveys were conducted in both areas during each year, except during 1977 when ships surveyed only the offshore area.

Data Collection

Aerial Data

Data collecting procedures used during the aerial surveys are described by SWFC (fn. 4), Jackson (fn. 5), Holt and Powers (1982), and Cologne and Holt (1984)[7]. As the airplanes traversed predetermined tracklines (Fig. 1), the observers recorded schools on and to either side of the lines. Observers searched through the bow window and from windows located on either side of the plane. The bow observer was responsible for detecting schools on the trackline (a path underneath the plane 0.19 km wide). The searching mode was halted if environmental or oceanographic conditions restricted the observer's view of the trackline or when the plane was diverted from the trackline for closer examination of a school. Additional schools detected during these diversions were not included in the density analysis.

Sea conditions were measured on the Beaufort scale (Bowditch 1966), which ranged from very flat, glassy seas (Beaufort 0 conditions) to rough seas with numerous large, white-capped waves (Beaufort 5 conditions). Sun location was described by horizontal and vertical position relative to the bow observer (Holt 1983a). These were recorded for each segment of effort.

Biological and environmental data were recorded at each sighting (Holt and Powers 1982). Data included species identification, school size estimates, sea state, sun position, and perpendicular distance to the school from the trackline. School size estimates consisted of an observer's "best" estimate plus an estimate of the minimum and maximum range.

Ship Data

Shipboard collection procedures are described in the various cruise reports (unpublished documents available from the SWFC) and by Holt (1983b). Procedures and data recorded on shipboard surveys were similar to those for aerial surveys. Two observers used binoculars located on each side of the ship to search from directly ahead to abeam of their respective sides of the ship. Starting in 1979, sea state was recorded at the beginning of each effort segment (leg). Sun position was recorded during the 1982 and 1983 ship surveys.

The bearing (θ) and radial distance (r) to a school from the ship were recorded, and perpendicular distance (y) was then calculated as $y = r \sin \theta$. In surveys conducted before 1980, observers rounded estimates of sighting angles to multiples of 5° or 10°, and radial distances to multiples of 185 m (0.1 nmi) within the first 1.85 km (1 nmi), and to 0.93 km (0.5 nmi) multiples at larger distances (Fig. 2). During training, observers on the 1980 surveys were told of previous rounding inaccuracies and instructed to make estimates as precise as possible. However, they were still unable to make precise visual estimates of angles and distances for schools recorded at great distances from the ship (Fig. 2). During the 1982 and 1983 surveys, estimates of bearing were recorded using a 360° graduated washer attached to the base of the binoculars, and the radial distances were measured using a graduated reticle enclosed in the right eyepiece of the binoculars (Holt 1983b).

[6]Au, D., W. Perryman, and W. Perrin. 1979. Dolphin distribution and the relationship to environmental features in the eastern tropical Pacific. Southwest Fisheries Center Status of Porpoise Stocks working paper SOPS/79/36, 59 p.

[7]Cologne, J., and R. Holt. 1984. Observer effects in shipboard sight surveys of dolphin abundance. Southwest Fish. Cent. Adm. Rep. No. LJ-84-30, 42 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

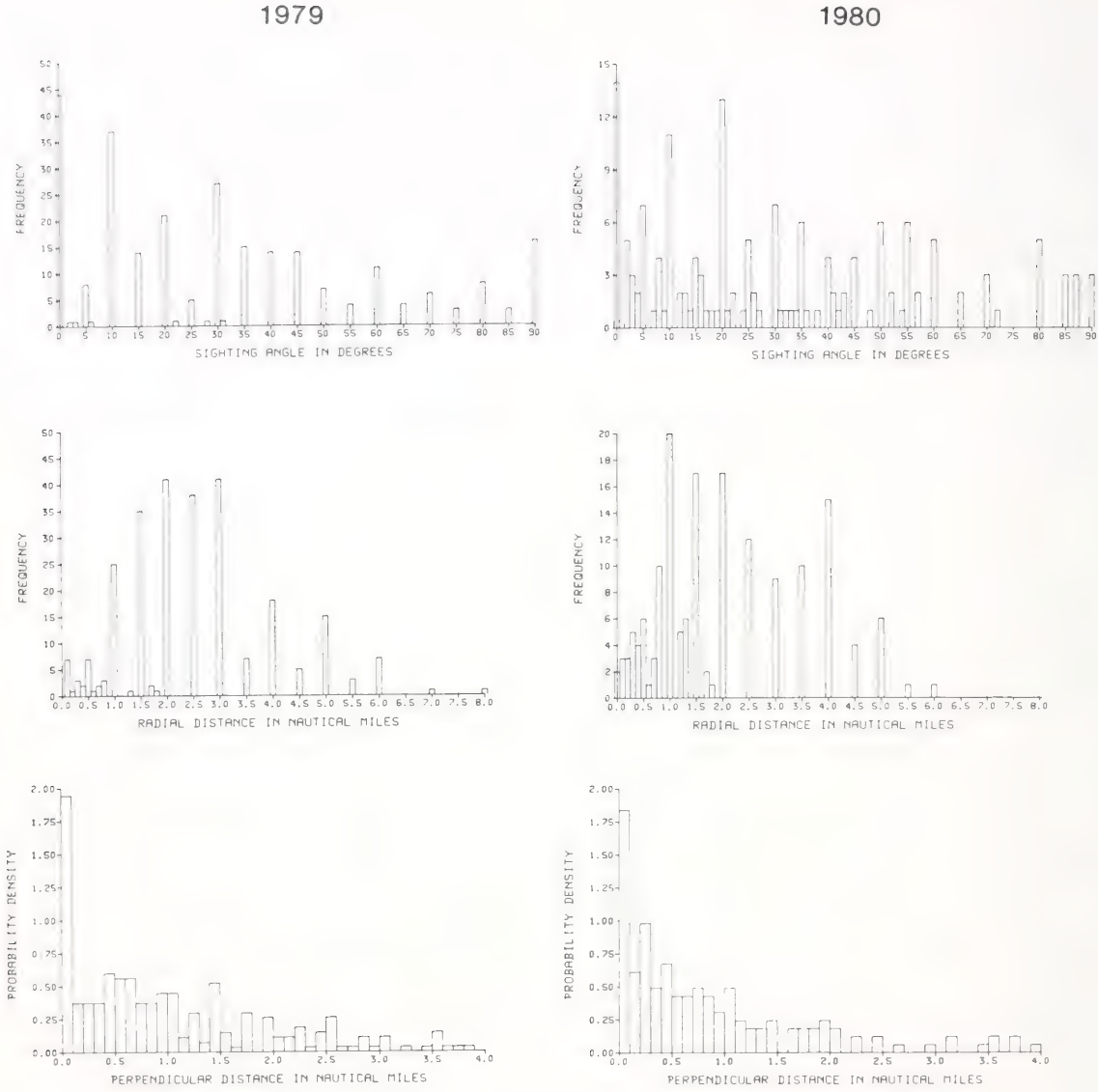

FIGURE 2.—Distribution of sighting angle, radial distance, and perpendicular distance from 1979, 1980,

With this system, the rounding to convenient values was not as evident (Fig. 2); however, measurements may still be inaccurate.

ANALYTICAL METHODS

Vessel data for area, sea state, sun glare, and observer performance strata were compared using rates of detection for all schools encountered within 2.13 km perpendicular distance of the ship (schools/1,000 km searched) and estimates of density of schools (schools/1,000 km^2). Similar comparisons of aerial data were completed using rates of detection for all schools encountered within 1.85 km perpendicular distance of the trackline, rates of detection for trackline schools, and estimates of school density.

Density estimates were made using line transect (LT) theory (Burnham et al. 1980). The basic equation (Seber 1973) is

$$D = \frac{n\, f(0)}{2L}$$

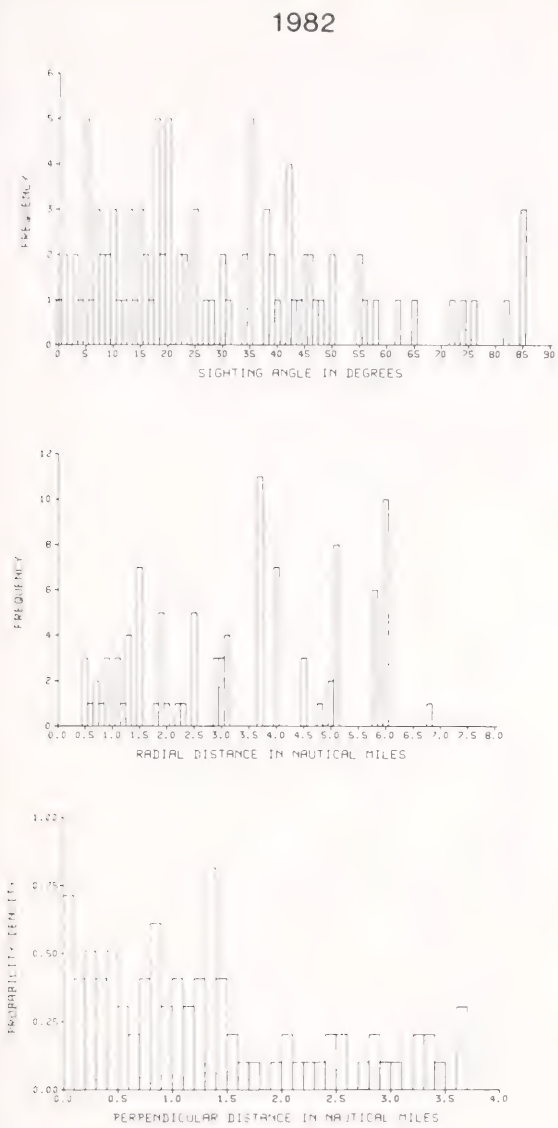

FIGURE 2.—*Continued*—and 1982 ship data.

where n is the number of schools sighted, D is the density of dolphin schools per km^2, L is the total linear distance searched (km), and $f(0)$ is a probability density function (*pdf*) evaluated at perpendicular distance, $x = 0$. The Fourier series (FS) model (Crain et al. 1979) was used to estimate $f(0)$ based upon criteria developed by Burnham et al. (1979). Burnham et al. (1980) is recommended for a full presentation of the FS model and for variance estimation.

Several assumptions must be met for valid use of LT theory. I investigated three of them for this study: 1) schools directly on the trackline are never missed, 2) schools do not move in response to the approaching ship or plane; and 3) no systematic measurement errors occur. All three assumptions have been made in analyzing previous aerial survey data (Holt and Powers 1982); however, field studies have subsequently been conducted to investigate the ability of observers to detect trackline schools (Holt 1983a), and whether or not dolphins avoid approaching ships (Au and Perryman 1982; Hewitt 1985). In addition, assumption 3 was not accepted because an inordinately large number of schools detected from the ships was recorded on the trackline.

Data Treatment

All species of dolphins encountered in the study area were included in the analyses. Of these, only schools with a mean minimum or mean best estimate of more than 14 animals were used because my field experience indicated that the probability that all animals in a school of at least this size would be submerged at one time, and hence undetectable, was very small. In addition, species affected by the fishery generally occur in schools with more than 14 animals.

During the first 18 of 20 flights of the 1979 aerial survey, two independent teams of three observers each searched for dolphin schools. Members of each team always searched for dolphins during the same time, alternating with the other team.

For aerial and 1979-83 ship data, observers recorded sea state conditions according to individual Beaufort, but during analyses, I grouped the data into 1) a "calm" sea state category: seas without whitecaps (Beaufort conditions 0-2) or 2) a "rough" sea category: seas with whitecaps (Beaufort conditions 3-5). Data for Beaufort conditions >5 were omitted from the analyses. The presence of whitecaps was important because animal splashes were used as sighting cues during calm conditions but could not be easily distinguished from whitecaps during rough conditions.

For aerial data and 1982-83 ship data, sun glare effects were investigated by classifying effort at various sun positions into "good" and "poor" categories depending on the amount of sun glare on the trackline (see Holt[8] for method used

[8]Holt, R. 1984. Testing the validity of line transect theory to estimate density of dolphin schools. Southwest Fish. Cent. Adm. Rep. No. LJ-84-31, 56 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

to record position of sun relative to the platform and for criteria used to define sun categories for aerial data). Criteria used for ship data were based upon observations recorded during a subsequent ship survey (Hohn[9]). Hohn found poor sun conditions on the trackline only when horizontal sun position was 12 and vertical position was 1, 2, or 3 or when clouds were accompanied by fog or rain. All other effort was defined as occurring during good conditions.

In order to apply the Fourier series (FS) model to aerial and ship data, I structured the data by 1) selecting appropriate interval widths for grouping the perpendicular sighting distributions (data cutpoints), 2) choosing a maximum observation distance perpendicular to the trackline (truncation point), 3) developing criteria to select the appropriate number of terms for the FS model, and 4) choosing the type of transformation to use in compensating for measurement error in the shipboard data.

Based on a subset of the ship data (Holt[10]), I used an interval width of 0.37 km (0.2 nmi) and truncated the perpendicular distance distributions at 3.7 km (2.0 nmi). Since perpendicular distance distributions for the ship data, and also to a lesser extent for aerial data, have very prominent modes or "spikes" at the origin, existing criteria to select the appropriate number of terms in the FS model were unsatisfactory. Therefore, I selected the model which provided the best visual fit to the distributions near the origin (Holt fn. 10). This technique was easily applied and was consistent among data sets. For use of the technique I assumed that the sizes of the spikes near the origins of the perpendicular distance distributions were indicative of relative density among the data sets. To minimize the effects of recording errors, the data were smoothed using the technique "smearing" (Butterworth 1982; Hammond 1984).

Based on previous investigations of aerial data (Holt and Powers 1982), I selected a truncation point of 1.94 km (1.05 nmi) and an interval width of 0.19 km (0.1 nmi) for the aerial data. I used the same technique as used for ship data to select the appropriate number of terms in the FS models; however, the aerial data were not smoothed because there was no evidence that the data contained estimation errors as did the ship data.

An estimate of density in the total area ($\hat{D}_c$) was calculated by combining the aerial inshore ($\hat{D}_i$) and ship offshore ($\hat{D}_0$) density estimates weighted by the relative sizes of the inshore (A_i) and offshore (A_0) areas as

$$\hat{D}_c = \frac{\hat{D}_i A_i + \hat{D}_0 A_0}{A_i + A_0}$$

The estimate of variance of $\hat{D}_c$ is

$$\hat{Var}(\hat{D}_c) = \frac{A_i^2 \hat{Var}(\hat{D}_i) + A_0^2 \hat{Var}(\hat{D}_0)}{(A_i + A_0)^2}$$

RESULTS

Factors Affecting Density Estimates

Aerial Data

Density estimates for the aerial data in the inshore area during calm seas or with minimal sun glare were more than twice the estimates for data taken during rough seas or poor sun conditions (Table 1). Differences in estimators were even greater for sea state and sun glare interaction effects. These differences may have occurred because observers failed to detect trackline schools during poor conditions or because sea state conditions were spatially confounded with distance from shore. Therefore, these differences may be reflecting a decreasing onshore-to-offshore density gradient. This was investigated by partitioning the inshore aerial data into "coastal" and "offshore" bands for each Beaufort sea state (Fig. 3) and sun glare condition (Fig. 4). Sufficient data were not available in each band to stratify detection rates by each sun and sea state interaction category.

Sea conditions during the aerial surveys were rougher offshore than nearshore. More searching was done in the coastal band during low Beaufort states, whereas more searching was done in the offshore band at higher Beaufort states (Fig. 3). The rates of detecting dolphin schools were higher at each corresponding Beaufort state in the coastal band than in the offshore band (Fig. 5). The rates of detecting trackline schools were generally higher in the coastal band; however, these rates were based upon very few

[9]A. Hohn, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. January 1985.

[10]Holt, R. 1984. Estimation of density of dolphin schools in the eastern tropical Pacific Ocean using line transect methods. Southwest Fish. Cent. Adm. Rep. No. LJ-84-32, 72 p. National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—Estimates of school density made during all conditions and during calm and rough seas using aerial and ship data; estimates made during good and poor sun condition using aerial data. Estimates are made for data in the inshore, offshore and total areas. Estimates for all conditions were calculated using 1977 through 1983 data and estimates for sun and sea state conditions were calculated using 1979 through 1983 data. Estimates are also presented for data collected during an aerial experiment testing effects of sea state and sun glare.

Variable	Distance searched (km)	Number schools detected (n)	Density ($\hat{D}$) (schools/ 1,000 km^2)	SE (D)	CV (D)
Inshore area					
Aerial data					
all data	34,006	152	4.18	0.902	0.216
calm seas	8,920	70	8.48	2.198	0.259
rough seas	25,086	82	2.71	0.611	0.255
good sun	11,994	74	6.57	1.504	0.229
poor sun	22,012	78	2.87	0.505	0.176
calm-good	3,026	30	12.64	5.290	0.418
calm-poor	5,894	40	6.24	2.311	0.370
rough-good	8,967	44	4.29	1.202	0.280
rough-poor	16,118	38	1.78	0.460	0.258
Ship data					
all data	27,840	379	4.47	0.514	0.115
calm seas	8,008	170	7.32	1.259	0.172
rough seas	14,668	149	4.05	0.772	0.191
Offshore area					
Ship data					
all data	46,567	322	2.04	0.263	0.129
calm seas	4,623	72	4.91	1.414	0.288
rough seas	20,976	99	2.01	0.435	0.217
All areas					
Ship data					
all data	74,407	626	2.95	0.253	0.086
calm seas	12,631	242	6.53	0.991	0.152
rough seas	35,644	248	3.02	0.445	0.147
Holt (text fn. 10) aerial experiment					
calm-good	1,414	37	29.18	7.357	0.252
calm-poor	3,014	81	23.78	5.888	0.248
rough-good	1,886	42	39.42	8.193	0.208
rough-poor	5,467	103	20.16	4.513	0.224

schools (18 trackline schools in the coastal and 10 schools in the offshore band were detected). Lower offshore estimates for data recorded under the same Beaufort state were consistent with a decreasing onshore-offshore density gradient.

Within each band, sea state conditions were also spatially stratified because the lower Beaufort conditions occurred mostly in the nearshore and northern regions of each band (Fig. 3). Predictably, detection rates for all schools within each band declined as the Beaufort condition increased. Because of the large variability inherent in small sample sizes and spatial stratification of searching effort at the various Beaufort conditions, comparisons of rates of detecting trackline schools did not yield consistent trends. For example, within both bands, the trackline detection rate for Beaufort 2 conditions was larger than for Beaufort 1 conditions. In the coastal band Beaufort 5 conditions had higher trackline detection rates than Beaufort 4 conditions and rates for Beaufort 4 were higher than rates for Beaufort 3 (Fig. 5).

Searching effort for aerial data during good and poor sun conditions was also confounded with distance from shore (Fig. 4) and thus with sea conditions. Most good sun conditions (78%) occurred in the coastal band, whereas 59% of all poor sun

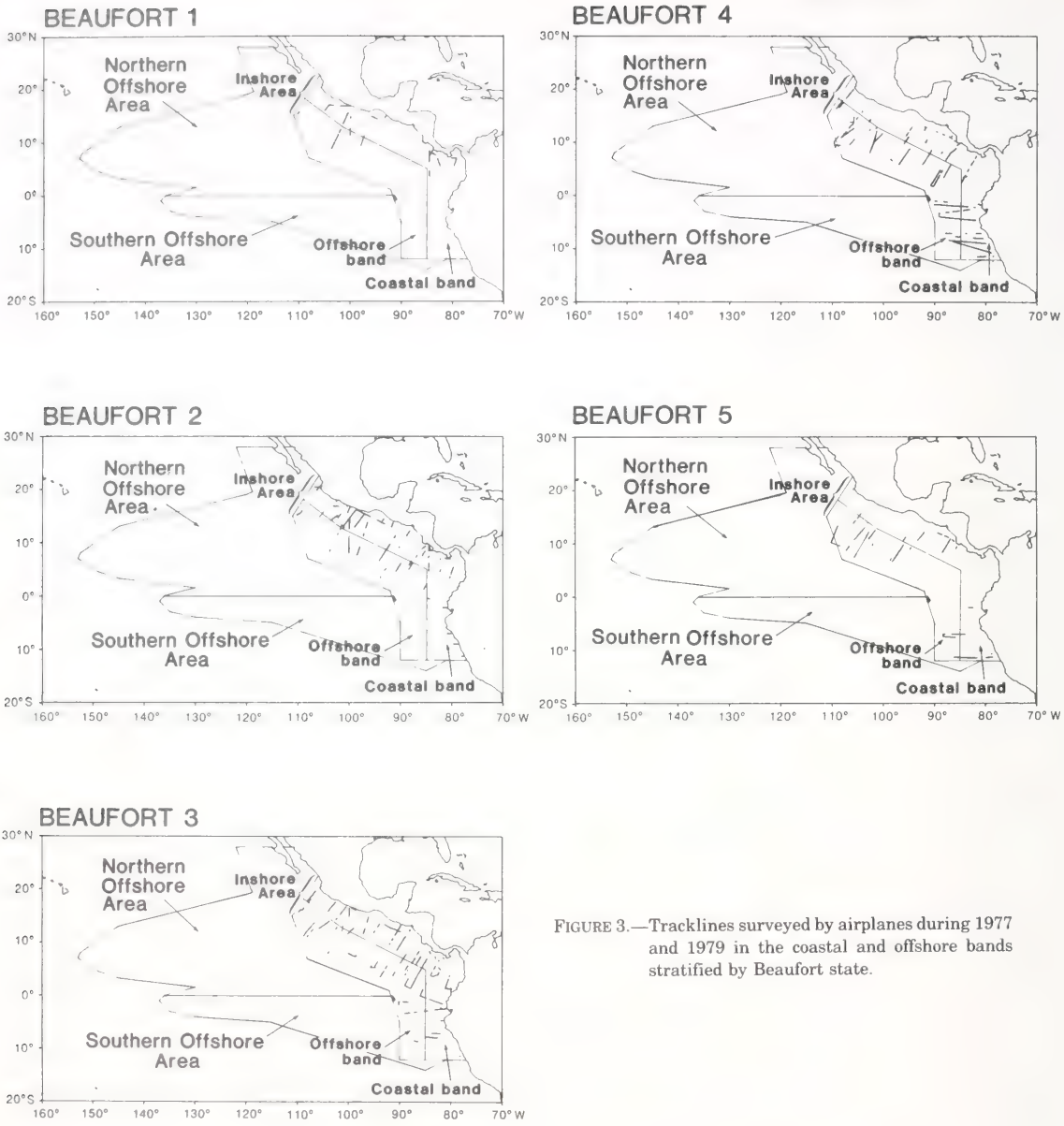

FIGURE 3.—Tracklines surveyed by airplanes during 1977 and 1979 in the coastal and offshore bands stratified by Beaufort state.

conditions occurred in the offshore band. This was because the general searching pattern was to begin searching on the westward, outbound leg in the morning, and then to turn the aircraft near noon and reach shore in late afternoon or night. Thus the sun was directly overhead or in front of the plane in the offshore reaches of the track and behind the plane in the nearshore areas.

Detection rates during good and poor sun conditions were higher in the coastal band than in the offshore band (Fig. 5), which was consistent with a hypothesized decreasing density gradient. Within the coastal band, detection rates during good sun conditions were greater than during poor sun conditions, but most of the poor sun data was gathered in the westward portion of the band (Fig. 4). In the offshore band, trackline detection rates during good and poor sun conditions were similar, but the rate during good sun conditions was based upon three sightings and only 8% of the effort.

Finally, I compared data collected by the ob-

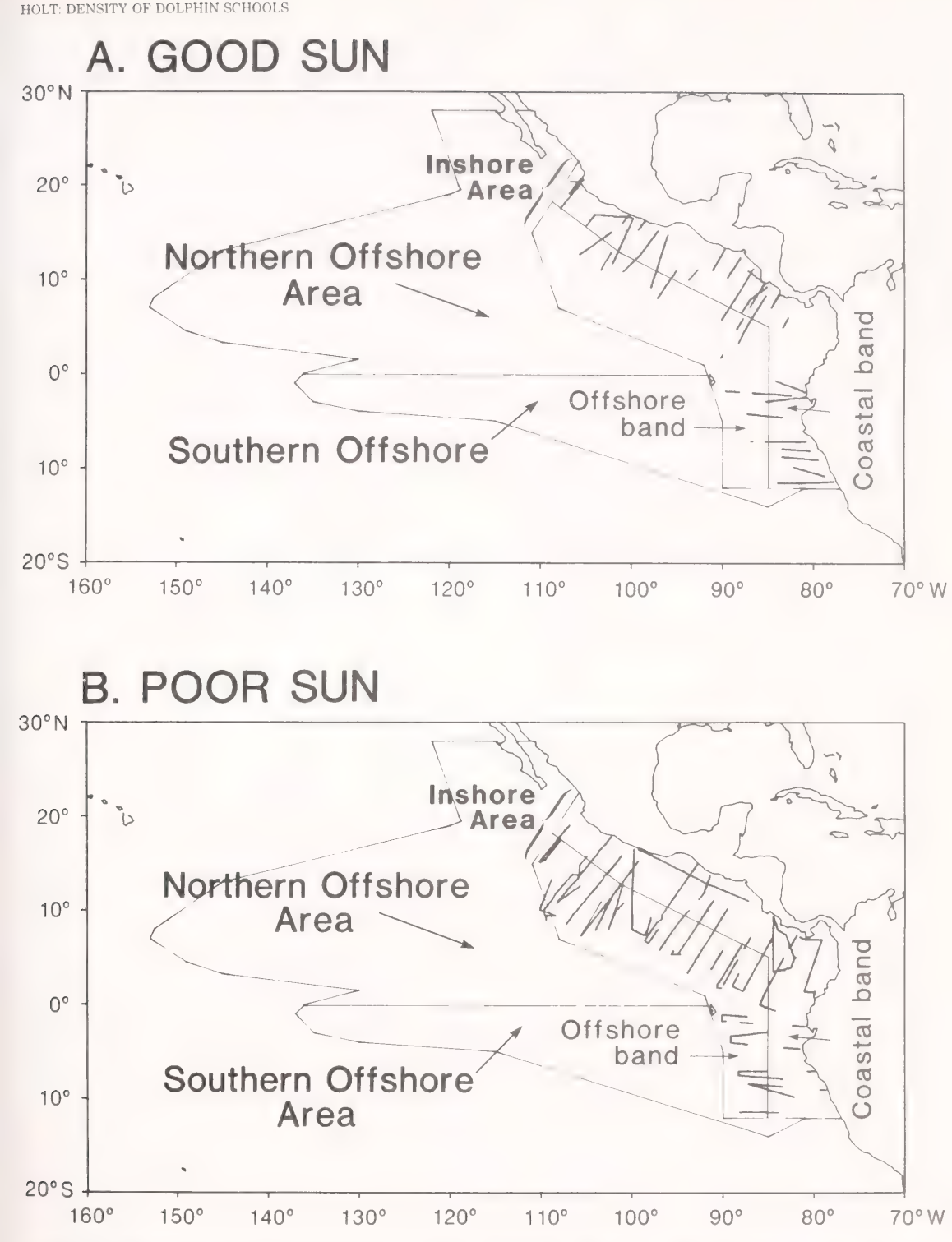

FIGURE 4.—Tracklines surveyed by airplanes during 1977 and 1979 during (A) good and (B) poor sun glare conditions in the coastal and offshore density bands.

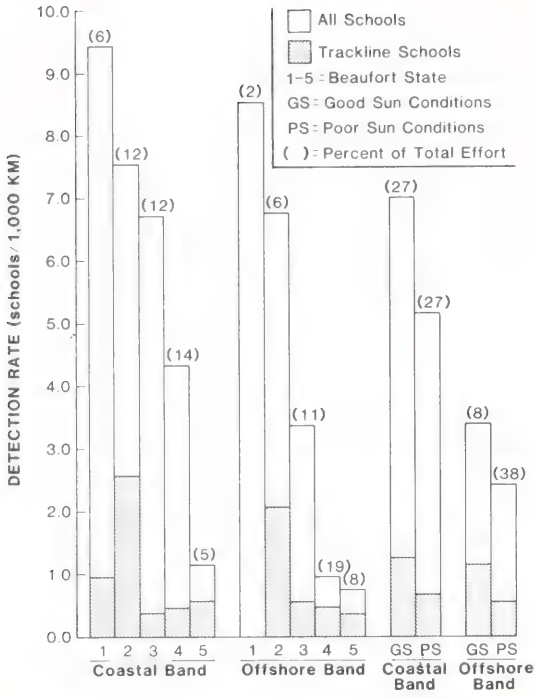

FIGURE 5.—School detection rates for aerial data in the coastal and offshore density bands for sea state and sun glare categories.

server teams to determine relative effects upon the density estimates. Team 1 and Team 2 searched approximately equal lengths of trackline (46% and 54% of the effort, respectively). No difference in performance of the two teams was evident: their rates of detecting schools, both on and off the trackline, and their estimates of school densities were approximately equal (Fig. 6).

Ship Data

The rates of detecting dolphins were greater during calm seas than during rough seas for the ship surveys from 1979 through 1983 (Fig. 7). The detection rate of dolphins during calm seas was more than twice the rate during rough seas in both the inshore and offshore areas. The ratio of calm sea to rough sea detection rates was larger in the offshore area than in the inshore area.

The offshore area was surveyed during rougher seas more than the inshore area (Fig. 8); seas were calm in the offshore area during only 17% of the effort as opposed to 35% for the inshore area surveys (Fig. 7). Dolphin density was lower offshore as indicated by lower offshore detection rates than inshore rates during either calm or rough seas (Fig. 7). The inshore-to-offshore-area detection ratios were 1.5 during calm seas and 2.0 during rough seas.

Sun glare had little effect on the shipboard estimates during either year because poor sun conditions occurred only during 6% of the 1982 and 8%

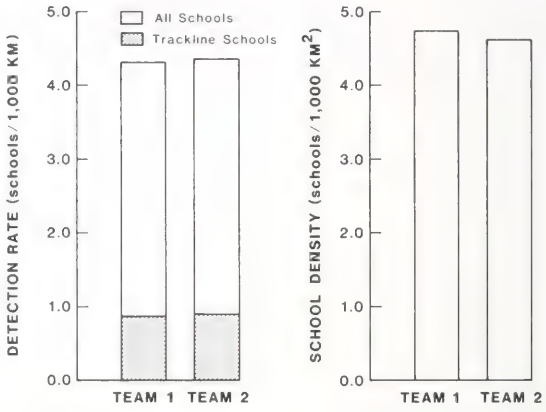

FIGURE 6.—School detection rates and density estimates for observer teams during the 1979 aerial survey.

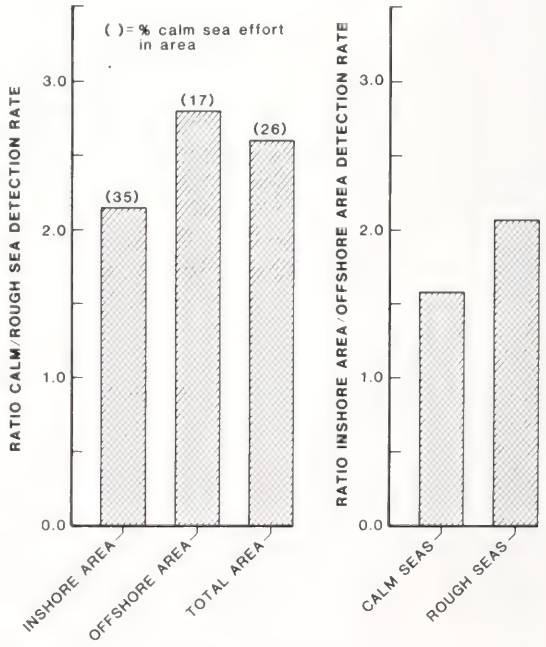

FIGURE 7.—Ratio of 1979-83 shipboard school detection rates for different sea states (calm sea versus rough sea) and area (inshore versus offshore). Detection rates computed with perpendicular distance data truncated at 2.1 km.

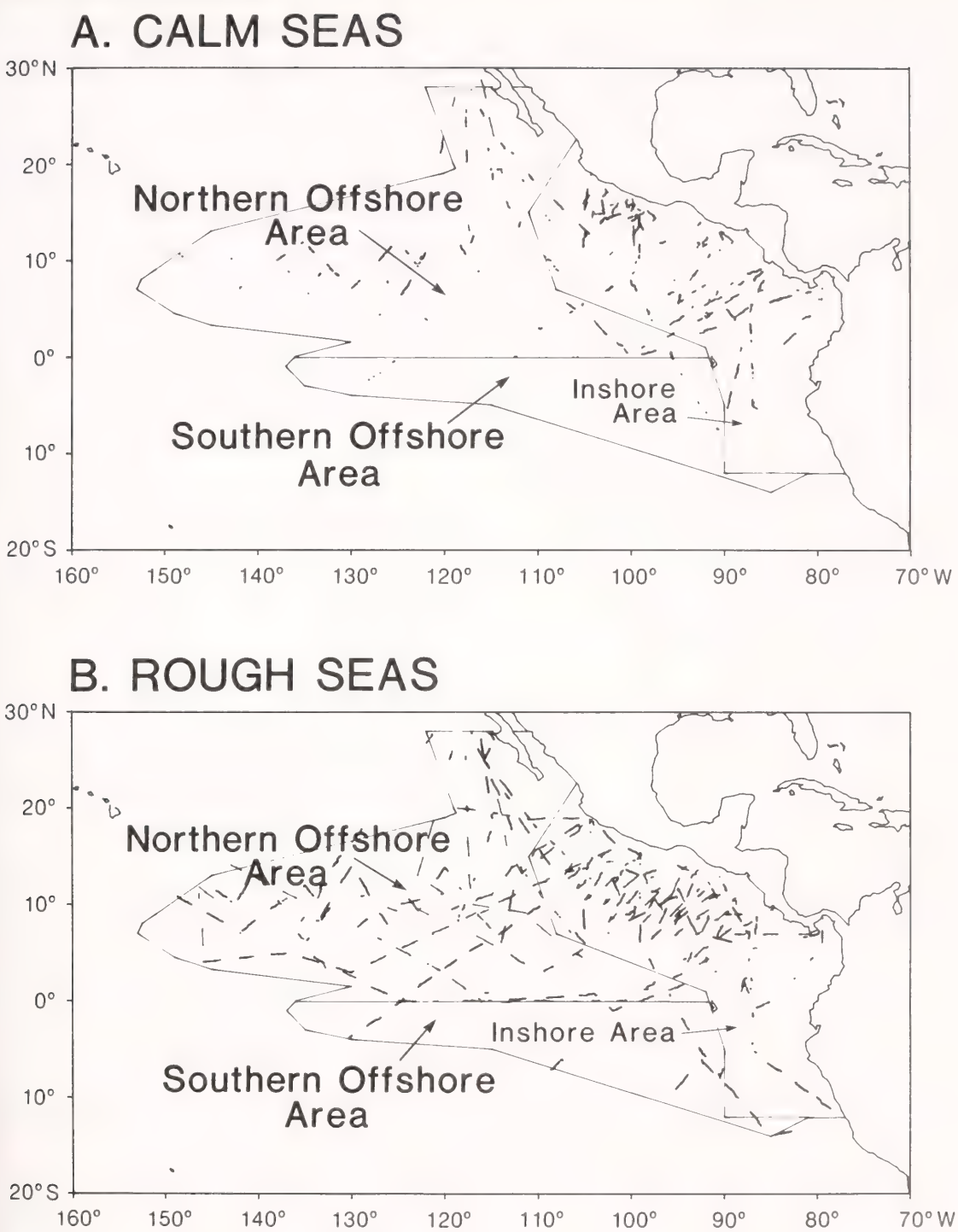

FIGURE 8.—Distribution of searching effort for the 1979-83 ship surveys during (A) calm and (B) rough conditions.

of the 1983 surveys. However, rates of detecting schools during good sun conditions were larger than during poor conditions (Fig. 9) and no schools were detected on the trackline during poor conditions.

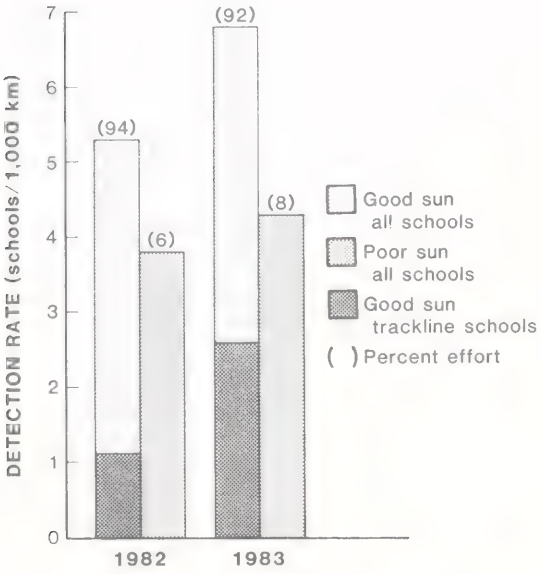

FIGURE 9.—School detection rates and relative density estimates during good and poor sun glare conditions for 1982 and 1983 ship data.

Density Estimates

Inshore Area

Aerial observers during the 1977 and 1979 surveys searched 34,006 km and detected 152 dolphin schools in the inshore area (Table 1). The estimate of school density using aerial data was 4.18 schools/1,000 km^2 with a standard error of 0.902.

From 1977 to 1983, shipboard observers searched 27,840 km in the inshore area and detected 297 schools (Table 2). Ship data yielded an estimate of density for the inshore area of 4.47 schools/1,000 km^2 with a standard error of 0.514 (Table 1). This was only slightly larger than the aerial inshore estimate.

Offshore Area

Observers aboard both vessels surveyed 46,567 km in the offshore area and detected 192 schools (Table 2). The estimate of density was 2.04 schools/1,000 km^2 with a standard error of 0.263 (Table 1).

Total Area

From 1977 to 1983, observers on both vessels searched 74,407 km in all areas and detected 489 schools (Table 2). The density estimate for all shipboard data was 2.95 schools/1,000 km^2 with a standard error of 0.253 (Table 1). The estimate of density using the aerial inshore estimate and the

TABLE 2.—School detection rates for 1977-83 ship data and for 1979-83 ship data stratified by sea state category in the inshore, offshore and total areas. Data were truncated at 2.13 km perpendicular distance.

Area/data source	Distance searched (km)	Percent (km) searched	Number schools detected	Percent schools detected	Detection rate (schools/ 1,000 km)	SE (detection rate)	Number days searched
Inshore area							
77-83 all data	27,840	100.0	297	100.0	10.67	0.82	173
79-83 calm seas	8,502	35.3	144	53.9	16.94	1.52	89
79-83 rough seas	15,609	64.7	123	46.1	7.88	0.92	124
Offshore area							
77-83 all data	46,567	100.0	192	100.0	4.12	0.50	251
79-83 calm seas	4,129	17.1	44	36.7	10.66	2.30	58
79-83 rough seas	20,015	82.9	76	63.3	3.80	0.56	134
Total area							
77-83 all data	74,407	100.0	489	100.0	6.57	0.47	417
79-83 calm seas	12,632	26.2	188	48.6	14.88	1.29	146
79-83 rough seas	35,624	73.8	199	51.4	5.59	0.54	256

ship offshore estimate was 2.71 schools/1,000 km^2 with a standard error of 0.334.

DISCUSSION

Onshore-Offshore Density Gradients

The onshore-to-offshore density gradient decreased based on aerial data in the inshore area and comparison of inshore and offshore density estimates. Offshore density estimates were only about one-half the inshore estimates (Table 1). Although sea state and sun glare conditions were confounded with distance from shore, comparisons of detection rates in the two inshore density bands for data stratified by Beaufort state or sun conditions indicated lower rates in the outer band (Fig. 5).

Fit of Fourier Series Model

Burnham et al. (1980) provided criteria for selecting the appropriate number of terms in the FS model. However, these criteria were not satisfactory for use with the aerial and ship perpendicular distance distributions, which had pronounced modes at the origin. Instead, I selected models which had the fewest terms but provided a good fit near the origin. This resulted in models with large numbers of terms. However, to the degree that the modes are representative of school density, my estimates of densities will be unbiased. Alternate statistical models need development which can fit data which lack a shoulder near the origin (i.e., data with pronounced modes at the origin). Buckland (1985) investigated several models but concluded that reliable estimation is not possible unless a shoulder exists.

Line Transect Assumptions

Aerial Data

Confounding of aerial sea state and sun condition data with distance from shore made it impossible to test the assumption that all trackline schools were detected during all viewing conditions. If viewing conditions had been homogeneous throughout the area, the density estimate calculated for calm sea and good sun conditions (12.64 schools/1,000 km^2) could be used for the inshore area (Table 1). This estimate is over 7 times the rough sea and poor sun estimate (1.78 schools/1,000 km^2). However, the calm seas and good sun condition effort occurred mostly in the northern nearshore region of the inshore area (Fig. 3, 4) where density may be high.

Consequently, Holt (fn. 8) conducted an aerial experiment in a relatively small area to test sea state and sun effects upon LT density estimates. The results indicated that sun glare adversely affected estimates of school density. The density estimate was 39% larger during good sun conditions than during poor conditions. Although density estimates were larger for calm sea data than for rough sea data, the differences were not significant.

The aerial experimental data (Holt fn. 8) may be used to estimate maximum bias for sun and sea state effects. The adjusted density estimate ($\hat{D}_A$) is

$$\hat{D}_A = \sum_{i=1}^{2} \sum_{j=1}^{2} \hat{D}_{ij} P_{ij} \left(\frac{\hat{D}'_{11}}{\hat{D}'_{ij}} \right)$$

where $\hat{D}_{ij}$ = Density estimate in survey area during ith sea state and jth sun condition,

P_{ij} = Proportion of effort in survey area with ith sea state and jth sun condition,

D'_{ij} = Experimental density estimate during ith sea state and jth sun condition determined from Holt (fn. 8).

In addition, i equal 1 denotes calm sea states and i equal 2 denotes rough sea states, and j equal 1 denotes good sun conditions and j equal 2 denotes poor sun conditions. An estimate of the sampling variance ($\mathrm{Var}(\hat{D}_A)$) using the Taylor approximation method is

$$\hat{Var}(\hat{D}_A) = \sum_{i=1}^{2} \sum_{j=1}^{2} P_{ij}^2 \left[\left(\frac{\hat{D}_{ij}}{\hat{D}'_{ij}} \right)^2 \hat{Var}(\hat{D}'_{11}) + \left(\frac{D'_{11}}{D'_{ij}} \right)^2 \hat{Var}(\hat{D}_{ij}) + \left(\frac{\hat{D}_{ij} \hat{D}'_{11}}{(\hat{D}'_{ij})^2} \right)^2 \hat{Var}(\hat{D}'_{ij}) \right].$$

The adjusted inshore density estimate is 4.51 schools/1,000 km^2 with a standard error of 1.107. This is an 8% increase over the unadjusted esti-

mate (Table 1). The adjusted combined estimate for the entire ETP was 2.81 schools/1,000 km^2 with a standard error of 0.152, a 4% increase from the unadjusted estimate.

Using the experimental results to adjust aerial estimates for sun glare (and possibly sea state), effects may be suspect because of differences in procedures followed and observational conditions encountered in the experiment and the surveys: 1) The wings on the aircraft used during the experiment were attached on the lower part of the fuselage, whereas wings on the 1977 and 1979 aircraft were attached to the upper part of the craft which allowed better lateral observation. 2) Procedures used to adjust for presence of sun glare during the surveys and the experiment differed. Observers during the surveys were instructed to stop searching if they believed conditions prevented their detecting trackline schools, but observers in the experiment searched during all conditions. 3) More rough seas were encountered during the surveys (74%) than in the experiment (62%). Also, more (46% as compared to 15%) of the surveys' total effort occurred at extreme Beaufort 4 and 5 conditions. Because of these uncertainties, I used the unadjusted density estimate to determine school densities.

Comparisons of the 1979 aerial observer teams' estimates did not indicate observers of either team missed dolphin schools on the trackline but both teams may have been equally affected by searching conditions. These results were consistent with results of the aerial experiment (Holt fn. 8) where comparisons of observer teams' performance also indicated no significant differences.

Ship Data

The density estimates calculated from calm sea data were larger than estimates calculated from rough sea data (Table 1). The difference was probably not due to missed trackline schools during rough seas. Schools on the trackline would probably be detected as the ship approached unless the schools avoided the approaching ship. In a ship-helicopter experiment Hewitt (1985) investigated the reaction of dolphins to survey vessels and found that dolphin schools only occasionally react to the approach of a vessel before they are detected by shipboard observers (1 of 12 schools).

The differences between calm and rough sea estimates may have resulted from actual differences in densities in areas surveyed during calm and rough sea states (Fig. 8). Another possibility is that estimation errors resulted from observers detecting schools at greater radial distances during calm conditions (mean radial distance was 4.16 km) than during rough conditions (mean radial distance was 3.55 km). Estimation of sighting angles and distances of schools at greater distances from the ship may have been less accurate and may have increased the probability of schools being erroneously recorded near or on the trackline.

Although sun glare was not shown to affect the shipboard density estimates, Cologne and Holt (fn. 7) found that shipboard observers tended to avoid searching areas with sun glare. However, because of the relatively slow speed of the ship and the dolphins and because sun glare at any specific time is usually concentrated in a small region of the observers' field of view, all regions may be observed without glare.

The occurrence of errors in angle and distance estimations may have positively biased shipboard estimates. An inordinate proportion of dolphin schools (25% of all schools) was recorded as being on the trackline. Smearing the perpendicular distance distributions helped alleviate the bias but may not have eliminated it.

Comparison of Aerial and Ship Estimates

The estimates of dolphin densities in the inshore and the total areas using only ship data were slightly larger than estimates which used aerial inshore data (Table 1). This is logical because ship surveys were designed to overlap with aerial coverage in the inshore area and to provide systematic coverage of the offshore area. Therefore, they spent disproportionately more of their effort in the inshore area compared to its relative size and, within the inshore area, they spent disproportionately more effort in the northern nearshore region (Fig. 1), which has relatively high dolphin density. Although the inshore area represented 31% of the total area, 37% of the ship's effort was in the inshore area. In addition, 61% of the inshore effort was in the northern inshore region which represented approximately 44% of the inshore area. During the aerial surveys a systematic survey of the inshore area was conducted. Therefore, the best estimates of densities in the inshore and total areas are estimates calculated using the unadjusted aerial inshore data.

Comparisons with Previous Density Estimates

Density of ETP dolphin stocks have been estimated previously (SWFC 1976[11]; Holt and Powers 1982). The methods I used to calculate estimates were similar to those used by Holt and Powers. Therefore, differences that they noted between their assessment in 1979 and the SWFC 1976 assessment are also applicable to comparisons between the SWFC 1976 assessment and this study. My estimates differ from the 1979 estimates in that mine include

1) schools where either the observers' "best" or "lowest" estimate of mean school size was more than 14 animals (the 1979 assessment included only schools with "best" estimates),
2) use of the 1977 aerial data in the inshore density estimate,
3) ship data collected in 1977, 1979, 1980, 1982, and 1983 (the 1979 assessment included only 1979 ship data),
4) investigation of aerial and ship data for effects of sun, sea state, and observer performance,
5) application of LT methods to ship data to calculate density estimates.

Density estimates calculated in this study were similar to those presented in the 1979 assessment (Holt and Powers 1982). My inshore and offshore estimates were 4.18 and 2.04 schools/1,000 km^2, respectively, with standard errors of 0.902 and 0.263. Holt and Power's estimates were 3.51 and 1.89 schools/1,000 km^2, respectively, with standard errors of 0.590 and 0.766.

CONCLUSIONS

LT methods were used on 1977 and 1979 aerial survey data to estimate dolphin density in the inshore area at 4.18 schools/1,000 km^2. LT methods applied to 1977-83 ship data yielded an estimate of offshore dolphin density of 2.04 schools/1,000 km^2. By weighting aerial inshore and ship offshore data by the respective size of the two areas, the total dolphin density was estimated at 2.71 schools/1,000 km^2.

I investigated differences among densities at different visibility conditions for aerial data, but results were inconclusive owing to confounding of the factors with density gradient (area from shore). Adjusting the data for sea state and sun conditions increased the inshore aerial density estimate 8% and the total density estimate by 4%.

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RESEARCH VESSEL SURVEY DESIGN FOR MONITORING DOLPHIN ABUNDANCE IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

During 1986 the National Marine Fisheries Service began conducting long-term research ship surveys to determine status of spotted dolphin, *Stenella attenuata*, stocks in the eastern tropical Pacific. This is the main dolphin species taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery. We use research vessel survey data collected from 1977 to 1983 to investigate the annual changes in spotted dolphin population size that could be detected given various levels of research vessel survey effort during specified time periods for several levels of statistical error.

We find that two research vessels each operating for 120 days per year for 5 years (six surveys) could detect a 10% annual rate of decrease in dolphin abundance (a total 41% decrease over 5 years) with alpha and beta error levels of 10%. Adding a third vessel would provide better coverage of the dolphins' range, but would allow only a slightly lower rate of decrease to be detected (an 11% annual rate, for a total decrease of 44%). These numbers point out the difficulty of detecting even major changes in spotted dolphin population size with present survey methods. Alternatives are discussed, but all either cost more money, require a longer time to detect a decline, or accept higher levels of statistical error.

The National Marine Fisheries Service (NMFS) has the responsibility of determining the status of dolphin stocks which are taken incidentally by the yellowfin tuna, *Thunnus albacares*, purse seine fishery in the eastern tropical Pacific (ETP) (Richey 1976[4]). The status of spotted dolphins, *Stenella attenuata*, is of special concern since it is the major species taken by the fishery (Smith 1979[5]). Of the spotted dolphins, the northern offshore stock is of more concern since it has been fished more frequently than the southern offshore stock. The spinner dolphin, *S. longirostris*, and the common dolphin, *Delphinus delphis*, are also taken. In addition, the striped dolphin, *S. coeruleoalba*, and the Fraser's dolphin, *Lagenodelphis hosei*, are occasionally caught but are difficult to distinguish from the other three species at a distance (Holt and Powers 1982). These 5 species are herein termed target species.

The NMFS conducted assessments of population status in 1976 (SWFC 1976[6]) and again in 1979 (Smith fn. 5) based on estimates of *absolute* stock abundance. The validity of the absolute estimates depended on several assumptions being met. Unfortunately, some assumptions, such as not allowing systematic errors in data recording or the assumption that dolphin schools do not move prior to being detected by shipboard observers, may not have been met and thus the assessments were not entirely satisfactory. An alternative approach for assessing stock status, therefore, is to use *relative* population estimates to detect trends in stock sizes over a long time period. Relative estimates can provide an assessment of stock condition as long as the biases in the abundance estimates are consistent over the sampling period. Therefore, the NMFS is presently considering using annual estimates of population abundance as relative estimates to detect declines in population size of spotted dolphins during a sampling period of at least 5 years.

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In this paper, we investigate the annual changes in the size of spotted dolphin populations that can be detected given various levels of research vessel survey effort within specified time periods. We investigate how many research vessels, assuming 120 days searching per vessel per year, would be required to survey the physical area inhabited by the major stocks. We also investigate how many vessels would be required to detect various levels of population declines in spotted dolphins during 5 years or, given fixed number of vessels, how many years of survey effort it would take to detect various population declines or, given fixed number of vessels for fixed number of years, the probability of detecting a decline (i.e., the power). We use historical data and current abundance techniques to predict variability of data which will be collected during the sampling period.

AREA INHABITED AND DATA SOURCES

For our analyses, the study area included the area described by Au et al. (1979)[7] as being inhabited by the target species (Fig. 1). The area north of lat. 20°N was excluded because spotted dolphins do not usually occur there. We partitioned the study area into four strata: the inside, middle, and west strata, which are located north of lat. 1°S, and a south stratum. The three northern strata were collectively termed the north area and all strata were termed the total area. In addition, a calibration area was defined as including part of the inside stratum (Fig. 1).

Data used in our analyses were collected from 1977 through 1983 by scientific observers aboard the NOAA ships *David Starr Jordan* and *Townsend Cromwell*. Survey coverage from the two ships for all years combined was thorough (Fig. 1). Data collected for each school included estimates of dolphin school size, species composition, and line transect observations, which we used to calculate density estimates.

SURVEY COVERAGE

We investigated the physical coverage of the area that is possible when using 1, 2, or 3 ships for

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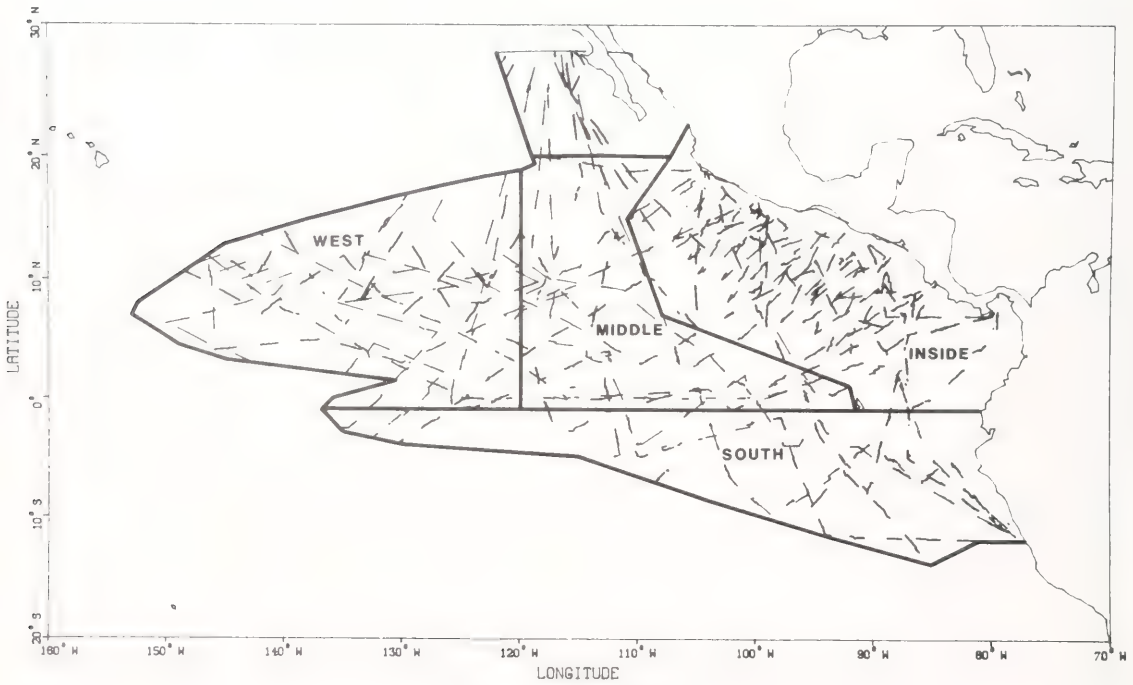


FIGURE 1.—Research vessel tracklines in each stratum during 1977 through 1983.

120 days each by plotting hypothetical tracklines. Approximately 370 km (200 nautical miles) of trackline could be covered in each survey day; with searching restricted to daylight hours, only about one-half of this distance would be searched. Approximately 40,700 km of trackline could be covered by each ship with less than 50% of this distance searched during daylight hours. Each ship's searching distance was allocated to each stratum by the square root of school density in the stratum. Effort of each ship was partitioned into 30-d segments between ports to meet logistical constraints of the vessels. We found that thorough coverage of the entire area was provided when three ships were used, two ships provided adequate coverage, and one ship provided very poor coverage with tracklines separated by large distances (Fig. 2).

DETECTION OF CHANGES IN POPULATION SIZE

Survey Design

The relationship among the number of samples, the rate of change, the precision of the population estimate, and the levels of alpha (type I) and beta (type II) statistical errors for several models of change and sample variability was investigated by Gerrodette (in press). We assumed that population size would change exponentially (constant rate per year). From Gerrodette's equation 15, using slightly different notation,

$$a(a+1)^2(a+2)[\ln(1-r)]^2 \geq 12(Z_\alpha + Z_\beta)^2 \sum_{i=0}^{\alpha} \ln\left[\frac{CV_0^2}{(1-r)^i} + 1\right] \qquad (1)$$

where a = number of years in the survey period,
r = annual rate of decrease,
Z_α = percentile of standardized normal curve for one-tailed Type I error,
Z_β = percentile of standardized normal curve for Type II error, and
CV_0 = coefficient of variation of the population estimate at the present population size.

In this formulation, r is a positive number, and, since the first survey occurs at time 0, the total number of samples (i.e., number of annual surveys) is $a + 1$. Note that the null hypothesis is one-sided, namely, that spotted dolphin abundance is decreasing. In addition to the annual rate of decrease (r), the total population decrease which would occur over the entire survey period was calculated as

$$\text{Total decrease} = [1 - (1 - r)^a].$$

The survey design to detect changes in dolphin abundance was investigated in three ways. Using Equation (1), we computed 1) the minimum number of years (a), given one to three ships per year and 120 searching days per ship per year, required to detect various annual decreases in spotted dolphin abundance; 2) the minimum proportional annual change (r) that could be detected in 5 years given one to three ships per year at various levels of alpha and beta; and 3) power ($1 - \beta$) or the probability of detecting various decreases in population size in 5 years, given one to three ships per year.

To use Equation (1), the relationship of $CV(\hat{N})$, the coefficient of variation of the population estimate, and n, the number of schools detected must be determined. In addition, the rate per day at which dolphin schools are expected to be encountered must be known. We used the 1977–83 research vessel data to investigate these factors assuming these data would be representative of data that we will obtain during the proposed sampling period of 1986–91.

Abundance Estimation

Relative estimates of population abundance of spotted dolphins in the north and total areas were calculated using two methods, methods A and B. In method A, density and mean school size estimates were calculated in each stratum and abundance was determined (Holt and Powers 1982) as

$$\hat{N} = \hat{P}_t \sum_{k=1}^{m} \hat{D}_k \hat{S}_{tk} \hat{P}_k A_k. \qquad (2)$$

In method B, density and mean school size estimates were calculated for data pooled for the entire area (north area or total area) and abundance was determined as

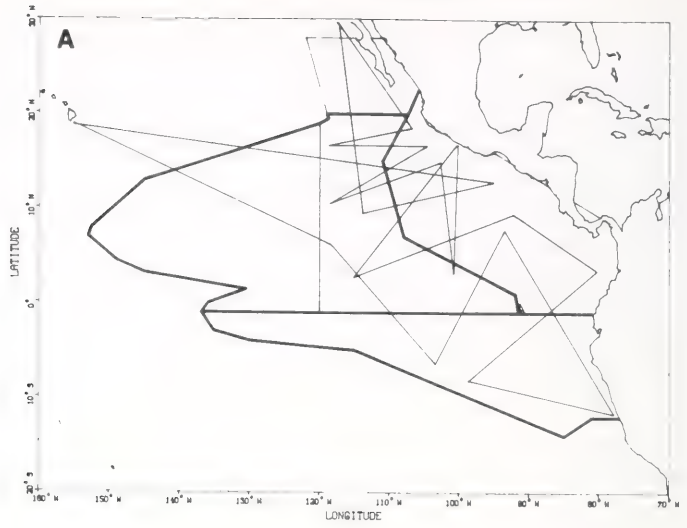


FIGURE 2.—Plot of hypothetical tracklines expected from use of one (A), two (B), or three (C) ships for 120 days each.

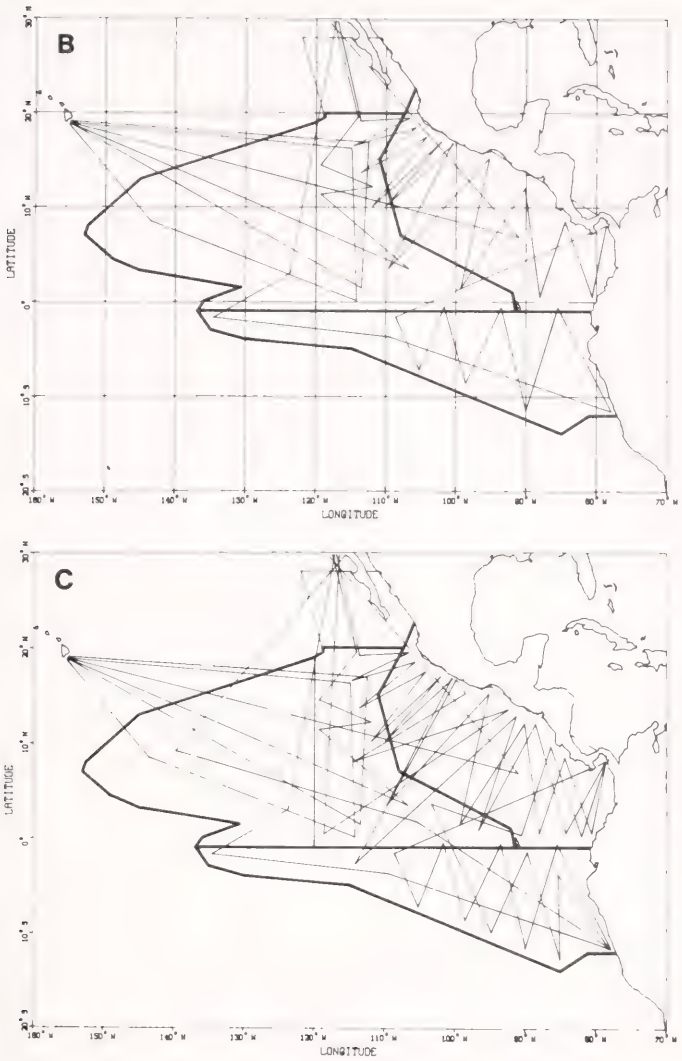
$$\hat{N} = \hat{P}_t \hat{D} \hat{S} \sum_{k=1}^{m} \hat{P}_k A_k. \quad (3)$$

where m = number of strata (3 for the north area and 4 for the total area),
k = 1, 2, 3, or 4 denotes the inside, middle, west, or south stratum, respectively,
$\hat{N}$ = estimated number of spotted dolphins in the survey area,
$\hat{D}$ = density estimate of number of schools of all dolphin species in the survey area (schools/1,000 km^2),
$\hat{D}_k$ = density estimate of number of schools of all dolphin species in the kth stratum (schools/1,000 km^2),
$\hat{S}$ = mean school size estimate for target species in the survey area (number of animals),
$\hat{S}_{tk}$ = mean school size estimate for target species in the kth stratum (number of animals),
$\hat{P}_t$ = proportion of all dolphins that were target species in the survey area,
$\hat{P}_k$ = proportion of spotted dolphins in the target schools in the kth stratum, and
A_k = area inhabited by all dolphins in the kth stratum.

The variance of $\hat{N}$ for Equation (2) was estimated using Taylor series expansion (Seber 1973) as

$$\begin{aligned} \text{Vâr}(\hat{N}) = \sum_{k=1}^{m} [&(\hat{S}_{tk} \hat{P}_t \hat{P}_k A_k)^2 \text{ Vâr}(\hat{D}_k) \\ &+ (\hat{D}_k \hat{P}_t \hat{P}_k A_k)^2 \text{ Vâr}(\hat{S}_{tk}) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_k A_k)^2 \text{ Vâr}(\hat{P}_t) \\ &+ (\hat{D}_k \hat{S}_{tk} \hat{P}_t A_k)^2 \text{ Vâr}(\hat{P}_k)] \ . \end{aligned} \quad (4)$$

The variance of $\hat{N}$ in Equation (3) was determined using Equation (4), but density and school size estimates that were calculated for the entire area



were substituted for the respective stratified estimates.

Specific formulae to estimate variables and associated theoretical variances in Equations (2) through (4) are from Burnham et al. (1980), Holt (1985,[8] in press) and Barlow and Holt (1986). Variances for estimates of school sizes and school densities were calculated using jackknife techniques (Miller 1974).

Since serial correlation among sampling units (days of effort) will yield biased estimates of standard errors using the jackknife method, we analyzed serial correlation of dolphin school detection rates among various combinations of successive days of effort. Analyses indicated that correlation was significant among successive single days but was not significant for periods of 2 or more days. Therefore, the data were grouped by 2-d increments for the jackknife analyses.

Estimates of spotted dolphin population abundance and values used in Equations (2) and (3) to calculate the estimates are presented in Table 1. CV ($\hat{N}$)s were smaller for estimates calculated using method B than for estimates using method A.

[8]Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin tuna fishery. Southwest Fish. Cent. Adm. Rep. No. LJ-85-20, 32 p. SWFC La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

TABLE 1.—School density of all dolphin schools, proportion of all schools which were target schools, mean school size of target schools, proportion of target animals which were spotted dolphins, area of each stratum, abundance and K values for spotted dolphins. SE and CV denote standard error and coefficient of variation, respectively. Methods A and B refer to different ways of pooling data on school size and density (see text).

Variable	Stratum				Area	
	Inside	Middle	West	South	North	Total
School density ($\hat{D}$) (Schools/1,000 km^2)	5.33	3.42	0.82	1.93	3.20	3.03
SE ($\hat{D}$)	0.87	1.13	0.30	0.39	0.54	0.51
CV($\hat{D}$)	16.3	33.1	37.2	20.2	17.0	16.8
Prop. target (P_t)[1]	—	—	—	—	0.775	0.775
Mean school size (S_t) (Number animals)	108.59	113.89	121.06	157.65	111.62	118.21
SE (S_t)	9.82	11.24	23.28	29.84	7.44	7.92
CV (S_t)	8.6	9.9	19.2	18.9	6.7	6.7
Area (km^2 * 10^6)	4.602	3.764	5.298	4.359	13.664	18.024
Prop. spotted (P_k)[2]	0.38	0.51	0.51	0.26	—	—
SE (P_k)[2]	0.039	0.048	0.048	0.085	—	—
Abundance and K Values						
Method A						
$\hat{N}$ (Animals * 10^6)					1.571	1.839
SE ($\hat{N}$)					0.283	0.294
CV ($\hat{N}$)					0.18	0.16
Sample size (n)					507	602
K					4.05	3.93
Method B						
$\hat{N}$ (Animals * 10^6)					1.761	2.081
SE ($\hat{N}$)					0.240	0.250
CV ($\hat{N}$)					0.14	0.12
Sample size (n)					507	602
K					3.06	2.94

[1]Source Holt (in press).
[2]Source Barlow and Holt (1986).

Relationship Between Var ($\hat{N}$) and Number of Schools Detected

In order to minimize the number of years required to detect a specific trend, Var ($\hat{N}$) should be as small as possible (Gerrodette in press). Var ($\hat{N}$) depends on the variance of the estimates of school size, school density, and proportions of the various dolphin species, as shown in Equation (4). Each of the variances of these estimates, in turn, depends on n, the number of sighted schools. Therefore, the dependence of Var ($\hat{N}$) on n must be known to calculate the number of sightings needed to attain a given level of precision (Var ($\hat{N}$)). We investigated the dependence of each of the individual variance terms on n.

Dependence of Var (S_{tk}), Var ($\hat{P}_t$), and Var (P_k) on n

Because $\hat{S}_{tk}$ is the mean of n individual school size estimates, its variance is Var ($\hat{S}_{tk}$) = Var (S_{tk})/n where Var (S_{tk}) is the variance of school size. The Var ($\hat{P}_t$) = $P_t(1 - P_t)/n$ where P_t is the true proportion of target schools among all dolphins. Var (S_{tk}) and $P_t(1 - P_t)$ are both constant with respect to n, so Var ($\hat{S}_t$) = $O(1/n)$ and Var ($\hat{P}_t$) = $O(1/n)$, where $O(1/n)$ means "of the same order as $1/n$" and implies that as $1/n$ approaches zero, the variance approaches zero at the same rate. Similarly, Var ($\hat{P}_{ik}$), which is also a proportion, is equal to $O(1/n)$.

Dependence of Vâr ($\hat{D}$) on n

The Vâr ($\hat{D}$), based on replicate tracklines (Burnham et al. 1980), is

$$\text{Vâr}(\hat{D}) = \hat{D}^2 \left[\frac{\text{Vâr}(n)}{n^2} + \frac{\text{Vâr}[\hat{f}(0)]}{[\hat{f}(0)]^2} \right] \quad (5)$$

where n is the number of sightings and $\hat{f}(0)$ is the

estimate of the probability density function of perpendicular distances extrapolated to the trackline. First,

$$\text{Vâr}(n) = \frac{R \sum_{i=1}^{R} (n_i - \bar{n})^2}{R - 1}$$

where R is the number of replicate lines of equal length (l). For R of moderate size, $R \cong (R - 1)$. Thus

$$\text{Vâr}(n) = \sum_{i=1}^{R} (n_i - \bar{n})^2 = O(\mathrm{R}).$$

This is because Vâr (n) is the sum of the variances of R independent values $(n_i, i = 1, 2, ..., R)$ each having the same expected variance. But $R = n/E(n_1)$, the total number of sightings divided by the expected number of sightings for a line of length l. Thus, $R = O(n)$, and

$$\frac{\text{Vâr}(n)}{n^2} = \frac{O(n)}{n^2} = O(1/n). \qquad (6)$$

Second, $\hat{f}(0)$ was estimated using a Fourier series (FS) model (Burnham et al. 1980); therefore,

$$\text{Vâr}[\hat{f}(0)] = \sum_{j=1}^{m} \sum_{k=1}^{m} \text{Cov}(\hat{a}_j, \hat{a}_k)$$

$$k = 1, 2, 3, ..., \text{and } k > j > 1$$

where the a's are the coefficients in the series

$$\hat{a}_k = \frac{2}{nw}\left[\sum_{i=1}^{n} \cos\left(\frac{k\pi x_i}{w}\right)\right] = O(1)$$

with x_i equal the perpendicular distance to the ith sighting and w equal the truncation point for the perpendicular distance. Therefore, we only need to know the dependence of cov(a_j, a_k) on n. If n is much larger than one, $(n - 1) \cong n$ and

$$\text{Côv}(\hat{a}_j, \hat{a}_k) = \frac{1}{n-1}\left[\frac{1}{w}(\hat{a}_{k-j} + \hat{a}_{k-j}) - \hat{a}_j \hat{a}_k\right]$$

$$= O(1/n).$$

Since $\hat{f}(0)$ estimates a quantity which is constant with respect to n,

$$\frac{\text{Vâr}[\hat{f}(0)]}{[\hat{f}(0)]^2} = O(1/n). \qquad (7)$$

Combining Equations (6) and (7) with Equation (5), $[\text{CV}(\hat{D})]^2 = O(1/n)$. This confirms discussions presented by Burnham et al. (1980).

In addition to investigating the theoretical dependence of $[\text{CV}(\hat{D})]^2$ on n, we tested its empirical dependence on n using the research vessel data which included 479 days of survey effort. Data were truncated at 3.70 km perpendicular distance from the ship. Paired days of shipboard searching effort were randomly selected using a uniform random number generator until the number of associated sightings (n) equaled or exceeded a previously selected sample size. Sample sizes selected were 20, 30, 40, 50, 60, 80, 100, 200, 500, and 1,000. The resultant perpendicular distance distributions were smeared (a data smoothing technique described by Butterworth 1982, Hammond 1984, and Holt fn.8), and density, variance, and coefficient of variation estimates were calculated for each data set. The simulation was completed three times for each value of n.

The relationship between CV $(\hat{D})$ and $1/\sqrt{n}$ (Fig. 3) was linear ($F_{\text{lack-of-fit}} = 0.83$; $P = 0.59$) with intercept not significantly greater than zero ($t = 1.56$; $P > 0.10$). This confirms the analytical result above, that CV $(\hat{D}) = O(1/\sqrt{n})$; however, as n increased, the probability of randomly selecting data from each of the 240 pairs of days (479 survey days) multiple times increased which may

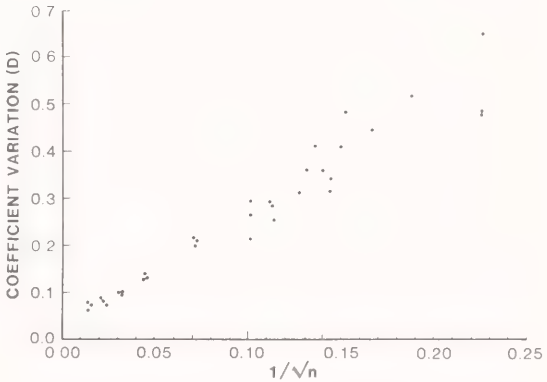


FIGURE 3.—Comparison of number of dolphin sightings $(1/\sqrt{n})$ and precision of the population estimate (CV(D)).

have biased CV ($\hat{D}$) if the distribution of sightings for the days were biased due to the effects of season or area. If we had included more large samples in our simulation, the linear relationship may not have been evident.

Calculation of K Values

Because all terms used to calculate Var ($\hat{N}$) equal $O(1/n)$ and Var ($\hat{N}$) is a linear sum of the terms, Var ($\hat{N}$) = $O(1/n)$ or CV ($\hat{N}$) = $O(1/\sqrt{n})$. Therefore, the relationship

$$\mathrm{CV}(\hat{N}) = K \setminus \bar{n} \tag{8}$$

can be used to determine the change in CV ($\hat{N}$) for various values of n, where K is a constant. This relationship is true if the number of schools sighted is proportional to population size. This seems to be a reasonable assumption, although a more complicated relationship between density and school size, based on dolphin social structure and its interaction with the fishery process, is possible. K values for spotted dolphins in the north and total areas were calculated for methods A and B using the 1977–83 data (Table 1). These K values were then used to determine CV ($\hat{N}$)s for specified values of n which would be expected assuming from one to three annual ship surveys.

Detection Rates

The number of expected sightings with use of one to three ships was calculated by computing detection rates as the average number of dolphin sightings per searching day. A day's searching effort generally consisted of searching from sunrise to sundown; therefore, we assumed most survey days covered approximately the same trackline distance. However, distance searched may vary inversely with rates of detecting dolphin schools because effort is halted so that observers can identify schools and make school size estimates. The number of survey days, and hence number of ships, required to obtain a specified CV ($\hat{N}$) was determined by dividing the number of required sightings by the rate of detecting schools.

Detection rates were caculated separately for data from the *Jordan* cruise and from the *Cromwell* cruise because of the wide disparity in detection rates of dolphins from the two vessels when operating simultaneously in the calibration area (Table 2). The *Jordan* has a much better platform from which to detect dolphins because its observation station was higher relative to the water and because the *Jordan* rode much smoother than the *Cromwell*. Pooled *Jordan* and *Cromwell* detection rates were calculated by standardizing the *Cromwell* rates to *Jordan* rates (Table 2) as

$$DR = \frac{R_j T_j + R_c T_c C}{T_j + T_c} \tag{9}$$

where DR = pooled standardized detection rate for all dolphin schools,
R_j = dolphin schools detected per day by observers aboard the *Jordan*,
R_c = dolphin schools detected per day by observers aboard the *Cromwell*,
T_j = days searched aboard the *Jordan*,

TABLE 2.—Detection rates of all dolphin schools from the *Jordan* and *Cromwell* in the calibration area and pooled standardized detection rates for both vessels combined calculated in each stratum. Standardized detection rates were calculated using the ratio of *Jordan* to *Cromwell* detection rates in the calibration area.

	Jordan (*J*)			*Cromwell* (*C*)			
Stratum/area	Number of schools (n)	Days searched (D)	n/D	Number of schools (n)	Days searched (D)	n/D	J/C ratio of detection rates
Calibration area	102	28	3.643	49	31	1.581	2.304
							Pooled standardized n/D
1. Inside	237	106	2.24	87	56	1.55	2.70
2. Middle	108	80	1.35	18	22	0.82	1.47
3. West	43	54	0.80	14	56	0.25	0.69
4. South	91	60	1.52	4	5	0.80	1.54
North area (Pooled strata 1-3)	388	226	1.72	119	128	0.93	1.87
Total area (Pooled strata 1-4)	479	282	1.70	123	132	0.93	1.84

T_c = days searched aboard the *Cromwell*, and

C = ratio of schools detected per day by observers aboard the *Jordan* in the calibration area during 1979 to schools detected per day by observers aboard the *Cromwell* in the calibration area during 1979.

The percent of searching days when one to three ships were used was allocated to each stratum (Table 3) by the square root of school density. The number of schools which would be expected to be detected based on the standardized detection rates then was calculated (Table 4).

TABLE 3.—Percent of searching days allocated by square root of density to each stratum in the north and total areas.

Stratum	North area	Total area
Inside	45.6	35.8
Middle	36.5	28.7
West	17.9	14.0
South	—	21.5

TABLE 4.—Number of days searched and number of schools detected per year of effort with use of 1, 2, or 3 ships allocated to the various strata by square root of density.

	North		Total	
Stratum	Number days	Number schools	Number days	Number schools
1 ship = 120 days				
Inside	55	149	43	116
Middle	44	65	34	50
West	21	14	17	12
South	—	—	26	40
Total	120	228	120	218
2 ships = 240 days				
Inside	110	298	86	232
Middle	88	130	68	100
West	42	28	34	24
South	—	—	52	80
Total	240	456	240	436
3 ships = 360 days				
Inside	165	447	129	348
Middle	132	195	102	150
West	63	42	51	36
South	—	—	78	120
Total	360	684	360	654

RESULTS

For either the north or total area, the same decrease in spotted dolphin populations can be detected 2 to 4 years earlier using method B, which uses pooled density and school size estimates, than when using method A, which uses estimates calculated for each stratum (Table 5). This is because large variances associated with the method A population size estimates occur due to small sample sizes in some strata. Therefore, method B was used in subsequent calculations.

The same number of years is required to detect a specific trend if the north or total areas are surveyed (Table 5). This result is true only if the 1977–83 data, which contain small sample sizes in the south stratum, are representative of future data. However, the northern offshore spotted dolphin stock occurs only in the north area and elimination of the south stratum will ensure better coverage of this north area, especially in the west stratum where sample sizes are minimal for applying the Fourier series model (Table 4). Therefore, subsequent calculations were made only for the north area. Annual population estimates for the northern stock would be biased only if substantial variation in the amount of dolphin migration between the north area and south stratum occurred during survey years.

TABLE 5.— Number of years required to detect an annual 5% decrease in spotted dolphin population size using 1, 2, or 3 ships and 2 different methods of pooling data. Method A utilized Equation (2) in text while method B utilized Equation (3). Alpha and beta levels equal 0.05, and effort was allocated to the various strata by square root of density. Number of schools expected to be detected each year determined using detection rates from Equation (9). K determined using Equation (8). CV ($\hat{N}$) denotes coefficient of variation of population abundance estimate.

Stratum	Number ships	Number schools	K	CV ($\hat{N}$)	Years required
North area					
Method A	1	228	4.05	0.27	17
	2	456		0.19	12
	3	684		0.15	11
Method B	1	228	3.06	0.20	13
	2	456		0.14	10
	3	684		0.12	9
Total area					
Method A	1	218	3.93	0.27	17
	2	436		0.19	12
	3	654		0.15	11
Method B	1	218	2.94	0.20	13
	2	436		0.14	10
	3	654		0.11	8

At the 5% error level, only rates of change of 11% per year or greater can be detected in a 5-yr survey period, even using three ships per year (Table 6). This is a rather high rate of decrease,

TABLE 6.—Minimum rates of annual decrease and minimum total decreases in spotted dolphin population size which could be detected in 5 years under different conditions. Changes were calculated for several alpha and beta levels, with a one-tailed test, using 1, 2, and 3 ships, for CV (N) determined using jackknife formulae, and data in the north area pooled over all strata (method B).

Number ships	CV (N)	Decrease per year	Total decrease
$\alpha = \beta = 0.05$			
1	0.20	0.19	0.65
2	0.14	0.13	0.50
3	0.12	0.11	0.44
$\alpha = \beta = 0.10$			
1	0.20	0.14	0.53
2	0.14	0.10	0.41
3	0.12	0.08	0.34
α β 0.20			
1	0.20	0.09	0.38
2	0.14	0.06	0.27
3	0.12	0.05	0.23

and would lead to a 44% reduction in population size over the 5-yr period. If two or one ship is used, however, the minimum detectable rates of decrease are higher still, 13% and 19%, respectively. When the power of the survey design is considered, the same dilemma is evident (Table 7). Even when three ships are used, the power is acceptably high only if the rate of decrease is at least 10% per year. The probability of detecting a 5% per annum decrease at a 5% alpha level, for example, is only 0.51. This means that with a probability of 0.49 we would conclude that no decrease had taken place, when in fact it had. Power is even less if only one or two ships are used.

Alternatively, we may have either to conduct the surveys for more than 5 years and/or relax the acceptable alpha and beta error level (Table 8). With three ships and 5% error levels, 5 years is sufficient to detect a 10% per annum decline, but 9 years are required to detect a 5% per annum decline and 13 years are required to detect a 3% per annum decline. For alpha and beta levels equal 0.10 or 0.20 and use of three ships, a 5% decrease can be detected in 7 or 5 years, respectively.

TABLE 7.—Power, or the probability of detecting a decrease in spotted dolphin population size during a 5-yr period. Power was calculated for surveys using 1, 2, or 3 ships, for various rates of annual and total population decrease, and for testing the regression of population size against time at various significance levels (α).

Number of ships	CV (N)	Rate of decrease per year	Total decrease	Power when α = 0.05	0.10	0.20
1	0.20	0.01	0.05	0.08	0.14	0.26
		0.03	0.14	0.15	0.25	0.41
		0.05	0.23	0.26	0.40	0.57
		0.10	0.41	0.62	0.75	0.86
2	0.14	0.01	0.05	0.09	0.16	0.29
		0.03	0.14	0.22	0.34	0.52
		0.05	0.23	0.42	0.56	0.73
		0.10	0.41	0.87	0.93	0.97
3	0.12	0.01	0.05	0.10	0.18	0.31
		0.03	0.14	0.27	0.40	0.57
		0.05	0.23	0.51	0.66	0.80
		0.10	0.41	0.94	0.97	0.99

TABLE 8.—Number of years required to detect various annual decreases and total declines of spotted dolphins calculated for several alpha and beta levels using 1, 2, and 3 ships. CV (N)s were calculated using jackknife formulae and using data in the north area pooled over all strata (method B).

Number ships	CV (N)	Decrease per year	Number years required	Total decrease
$\alpha = \beta = 0.05$				
1	0.20	0.01	39	0.32
		0.03	19	0.44
		0.05	13	0.49
		0.10	8	0.57
2	0.14	0.01	30	0.26
		0.03	14	0.35
		0.05	10	0.40
		0.10	6	0.47
3	0.12	0.01	27	0.24
		0.03	13	0.33
		0.05	9	0.37
		0.10	5	0.41
$\alpha = \beta = 0.10$				
1	0.20	0.01	32	0.28
		0.03	15	0.37
		0.05	11	0.43
		0.10	7	0.52
2	0.14	0.01	25	0.22
		0.03	12	0.31
		0.05	8	0.34
		0.10	5	0.41
3	0.12	0.01	23	0.21
		0.03	11	0.29
		0.05	7	0.30
		0.10	5	0.41
$\alpha = \beta = 0.20$				
1	0.20	0.01	24	0.21
		0.03	11	0.29
		0.05	8	0.34
		0.10	4	0.34
2	0.14	0.01	19	0.17
		0.03	8	0.22
		0.05	6	0.26
		0.10	3	0.27
3	0.12	0.01	17	0.16
		0.03	8	0.22
		0.05	5	0.23
		0.10	3	0.27

DISCUSSION

Our analyses indicate that our ability to detect changes in the size of spotted dolphin populations in the eastern tropical Pacific is not very great without substantial long-term ship time. This is not surprising given the vast area of ocean inhabited by the dolphins and the low sighting rate from ships. We feel our results represent a generally accurate picture based on available data. However, the analyses must be qualified by noting that the data used to generate these results were accumulated during all seasons over 5 years. Data collected in the future will come from surveys conducted at the same time each year and may be less variable. In addition, more precise data gathering techniques or data fitting models may become available. If so, these factors would yield greater ability to detect lower rates of decrease, greater power, and lower required number of years. On the other hand, the estimates of expected variance have dealt with survey precision (measurement error) only. If environmental variability is important, data collected in future surveys may be more variable than we have calculated. In long-lived animals with many year classes contributing to reproduction, however, environmental variability will tend to be less important than survey imprecision (Gerrodette in press).

The selection of appropriate alpha and beta errors levels depends on one's perspective. An alpha error would occur if we concluded that a decrease in dolphin abundance was occurring when in fact it was not. It is therefore of interest to the tuna industry to minimize this type of error. A beta error would occur if we concluded that no decrease in dolphin abundance was occurring when in fact it was. It is in the interest of conservation groups to minimize this type of error. As is well known in statistical theory, however, there is a trade off between the two types of error, a decrease in one leads to an increase in the other. In our analyses we have balanced the two types of error by making alpha and beta equal. We have also used a range of equal alpha and beta levels (0.05, 0.10, and 0.20) to illustrate how choice of error level can affect sampling design. Higher tolerance of error leads to lower rates of decrease which could be detected in shorter times, but, of course, one is less sure of the conclusions reached. Thus the choice of acceptable alpha and beta levels to use in detecting changes in spotted dolphin population size is a management decision based primarily on social rather than statistical criteria.

At least two ships are required to provide representative coverage of the survey area. Although use of a third ship provides better coverage, it does not substantially improve detection of population decreases. For alpha and beta levels of 0.05, a 5% per year decrease can be detected in 9 years with use of three ships or 10 years with use of two ships (Table 8). For other alpha and beta levels, use of the third ship only increases our ability to detect specific decreases by about 1 year. Given the annual cost of each ship, it would be more cost-effective to conduct the surveys for an additional year using only two ships. Another strategy is to conduct surveys less frequently than annually. Gerrodette (in press) provides a numerical example of this approach. For parameter values appropriate to spotted dolphins, conducting surveys less frequently than annually (every second or third year, for example) could save substantial ship time, but more years would elapse before a trend was detected.

If a 5% annual decrease in population size occurred, the number of spotted dolphins killed would have to be large. Assuming a spotted dolphin population of 2.5 million animals (Table 1) and disregarding natural mortality and reproduction, approximately 125,000 animals would be killed each year. The estimates of all dolphins taken by the fishery during each of the last few years are only about 40,000 animals per year (Hammond and Tsai 1983). It may be unreasonable to expect annual decreases at the 5% annual level; rather decreases of 3% or 1% per year would be more reasonable. If so, two ships would require at least 14 years to detect the decline (Table 8).

Nonetheless, the number of dolphins actually killed may exceed 40,000 animals per year because dolphin mortality aboard the unsampled trips of U.S. and non-U.S. registered vessels, which is assumed to be similar to that on the sampled trips, may in fact be substantially higher. In addition, the effects of chasing and capturing dolphins several times per year are not estimated in our analyses.

Techniques and data are presented in our paper to determine the optimal number of ships and number of years required to detect decreases in spotted dolphin populations in the eastern tropical Pacific. However, these techniques are applicable to investigate the amount of effort and time required to monitor changes in any appropriate population index for any species where sufficient

data exists or can be collected to determine reasonable estimates of coefficient of variation.

SUMMARY

Use of three ships provides excellent physical coverage of the eastern tropical Pacific dolphin area. Coverage using two ships appears adequate while use of one ship yields very sparse coverage.

Assuming alpha and beta levels of 0.05, use of two ships for each of 5 years will only allow us to detect a 13% annual decrease in spotted dolphin abundance. This means that the population could decline by 50% during the survey period before it could be detected. If three ships are used for 9 years, a 5% decrease per year could be detected.

Use of two ships instead of three only decreases our ability to detect specific trends by about 1 year. For alpha and beta levels of 0.05, use of two ships will allow detection of a 5% annual decrease in 10 years, instead of 9 with three ships.

The sampling period may be shortened if larger alpha and beta levels and larger annual decreases are acceptable. For alpha and beta levels of 0.10, use of two ships will allow detection of a 10% annual decrease after 5 years during which a 41% decrease in the population could occur.

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A TRAWL SURVEY METHOD FOR ESTIMATING LOGGERHEAD TURTLE, *CARETTA CARETTA*, ABUNDANCE IN FIVE EASTERN FLORIDA CHANNELS AND INLETS

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ABSTRACT

Five eastern Florida navigational channels were surveyed on a quarterly basis from November 1981 through August 1982. The purpose of the surveys was to provide estimates of loggerhead turtle abundance for each channel over all seasons of the year. Standard methods for estimating loggerhead turtle abundance from trawl samples were developed, and the probability of capture in a 30 m by 1,483 m substation ($\bar{P}$) was estimated to be 0.28 ± 0.05 (95% confidence level). Abundance estimates based on this probability of capture were then developed for each channel and survey. Of the channels surveyed, only Port Canaveral harbored significant concentrations of loggerhead turtles; populations ranged from 701 ± 291 turtles in February to a low of 38 ± 26 turtles in August. A few loggerhead turtles were captured in the other channels, but infrequency of occurrence suggested random encounters rather than areas of concentration.

In the western Atlantic Ocean, loggerhead turtles, *Caretta caretta*, forage throughout the warm waters of the continental shelf from Argentina northward to Nova Scotia, including the Gulf of Mexico and the Caribbean Sea (Carr 1952). On a seasonal basis, loggerheads are common as far north as the Canadian portions of the Gulf of Maine (Lazell 1980), but during cooler months of the year distributions shift to the south (Shoop et al. 1981). Sporadic nesting occurs throughout the tropical and warm temperate range of distribution, but the most important nesting areas are the Atlantic coast of Florida, Georgia, and South Carolina (Carr and Carr 1978). The Florida nesting population of *Caretta* has been estimated to be the second largest in the world (Ross 1982).

Although population levels of adult female loggerheads can be estimated from counts on nesting beaches, the remaining animals (males, subadults, and nonbreeding females) do not come ashore and are not readily available for census. To estimate the total number of loggerheads in an area, all segments of the population should be considered.

In the vicinity of Cape Canaveral, FL, loggerhead turtles congregate in the Port Canaveral ship channel (Carr et al. 1980). Because turtles can be captured and studied in this unique area throughout the year, the National Marine Fisheries Service (NMFS) has conducted surveys to monitor population levels and estimate relative turtle abundance. This study is a continuation and expansion of research efforts which began in 1978.

Presented are results of a 1-yr investigation conducted in response to requests from the U.S. Army Corps of Engineers (COE) and the U.S. Navy, to estimate sea turtle abundance and seasonality in five eastern Florida navigational channels. Animals captured in this study were subadults, adult males, and adult females. Population estimates of subadult turtles may prove to be particularly useful for management, as efficacy of conservation measures should be first evident in the population levels of the youngest cohorts.

Results of this study provide a reliable index of loggerhead turtle abundance for the study year and an alternative to population estimates based only on nesting females. Most importantly, for the first time, a standard method has been developed that provides sea turtle abundance estimates with approximate standard errors.

STUDY AREAS

Five eastern Florida navigational channels were surveyed on a seasonal basis over the study period. A description of the survey sites follows (each site is diagramed in Figure 1):

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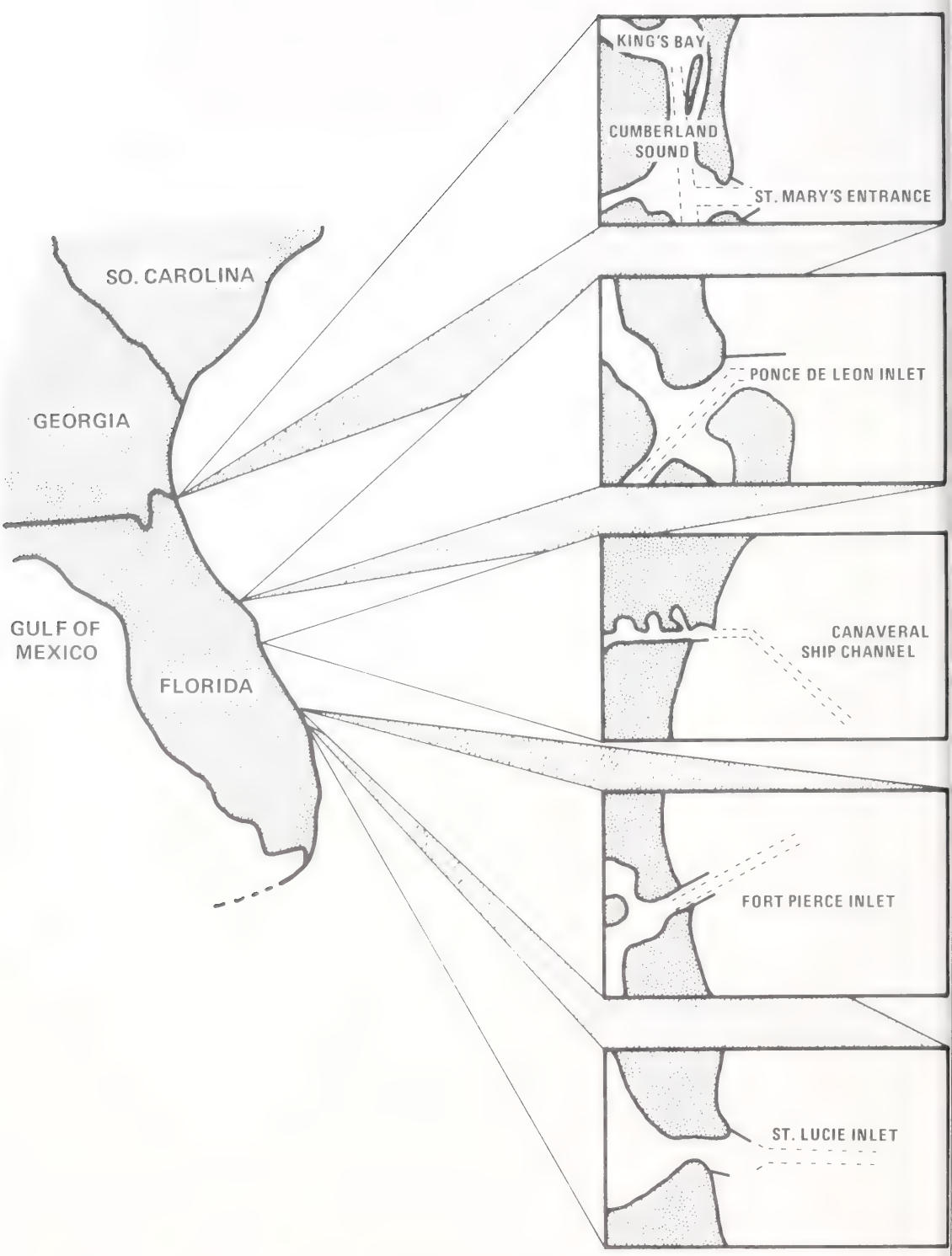

FIGURE 1.—Description of five eastern Florida navigational channels and inlets surveyed.

1) St. Mary's entrance to King's Bay (lat. 30°43′N, long. 80°20′W) is divided by the state boundary between Georgia and Florida and includes Cumberland Sound through which the Intracoastal Waterway connects King's Bay with the entrance channel. Mud predominates inside of the jetties, and mud and rock bottom are found in the channel offshore.

2) Ponce de Leon Inlet (lat. 29°04′N, long. 80°53′W), on the northeast coast of Florida, is a small inlet accessible only to small craft. A jetty protects the inlet to the north; inside the inlet a narrow channel leads to the Intracoastal Waterway. The substrate is hard sand and silt with scattered rubble.

3) The Port Canaveral ship channel is located on the central east coast of Florida (lat. 28°23′N, long. 80°33′W). The ship channel allows navigation from offshore, through a manmade inlet, into a protected harbor. A depth of 11 to 13 m is maintained by dredging. Soft mud and detritus bottom is found in the channel and sand-clay in the surrounding areas.

4) Fort Pierce Inlet (lat. 27°28′N, long. 80°16′W) is located on the south-central east coast of Florida. The channel allows navigation from offshore, through the inlet that is protected by jetties, into the Intracoastal Waterway. The bottom is hard sand and rubble.

5) St. Lucie Inlet, also on the south-central east coast of Florida (lat. 27°09′N, long. 80°07′W), is another small inlet with use limited to small craft. A completed jetty protects the north side of the inlet and a second jetty was under construction to the south during the survey periods. The substrate offshore is sloping hard sand and silt.

MATERIALS AND METHODS

Quarterly trawl surveys of the navigational channels were conducted from November 1981 through August 1982. During each survey, the Port Canaveral ship channel was sampled twice and the remaining four sites (St. Mary's entrance, Ponce de Leon Inlet, Fort Pierce Inlet, and St. Lucie Inlet) were sampled once. A standard 18 m "mongoose" fish trawl, spread by 3 m × 1 m trawl doors and equipped with mudrollers, was used throughout the study period.

Prior to the surveys, the boundaries of each channel were located using National Ocean Surveys charts and subdivided by a grid pattern for systematic sampling. Lengthwise, each channel was separated into 1,483 m stations which were divided into 30 m wide substations (Fig. 2). The number of substations in each station was dependent on channel width.

A systematic sampling scheme was devised to sample each channel substation: every other station was sampled in leapfrog fashion in one direction, and then the direction was reversed. The substation sampled within each station was determined by random drawing without replacement and sampling continued until all substations were occupied. This approach avoided the "edge effect", but allowed samples to be statistically treated as random (Milne 1959). Control stations outside the channel were sampled at all sites during each survey period.

In addition to standard survey procedures, experiments designed to estimate gear efficiency were conducted in the Port Canaveral ship channel. Following each survey, a substation with abundant loggerhead turtles was selected and a series of repetitive tows performed. All loggerheads captured during these experiments were tagged and released on station prior to the next tow. As this was essentially a "removal" method, any recaptures of loggerhead turtles tagged during the experiment were not considered as part of the catch and were excluded from analysis. Tows were continued in rapid order until two consecutive samples yielded zero catches or the working day ended.

ANALYTICAL PROCEDURES

The efficiency of the sampling gear was established before population estimates were computed. The probability of loggerhead turtle capture ($\hat{P}$) was estimated for each repetitive towing experiment using the formula:

$$\hat{P} = C_1/\hat{N}_0$$

where C_1 = catch on the first tow in the substation

$\hat{N}_0$ = estimated number of loggerhead turtles in the substation.

A regression of cumulative loggerhead turtle catch (Y) on catch per sample (X), expressed as $Y = b_0 + b_1X$, was used to estimate (N_0) based on the relationship: $\hat{N}_0 = b_0$. The estimated variance of N_0 was calculated according to procedures of Kleinbaum and Kupper (1978):

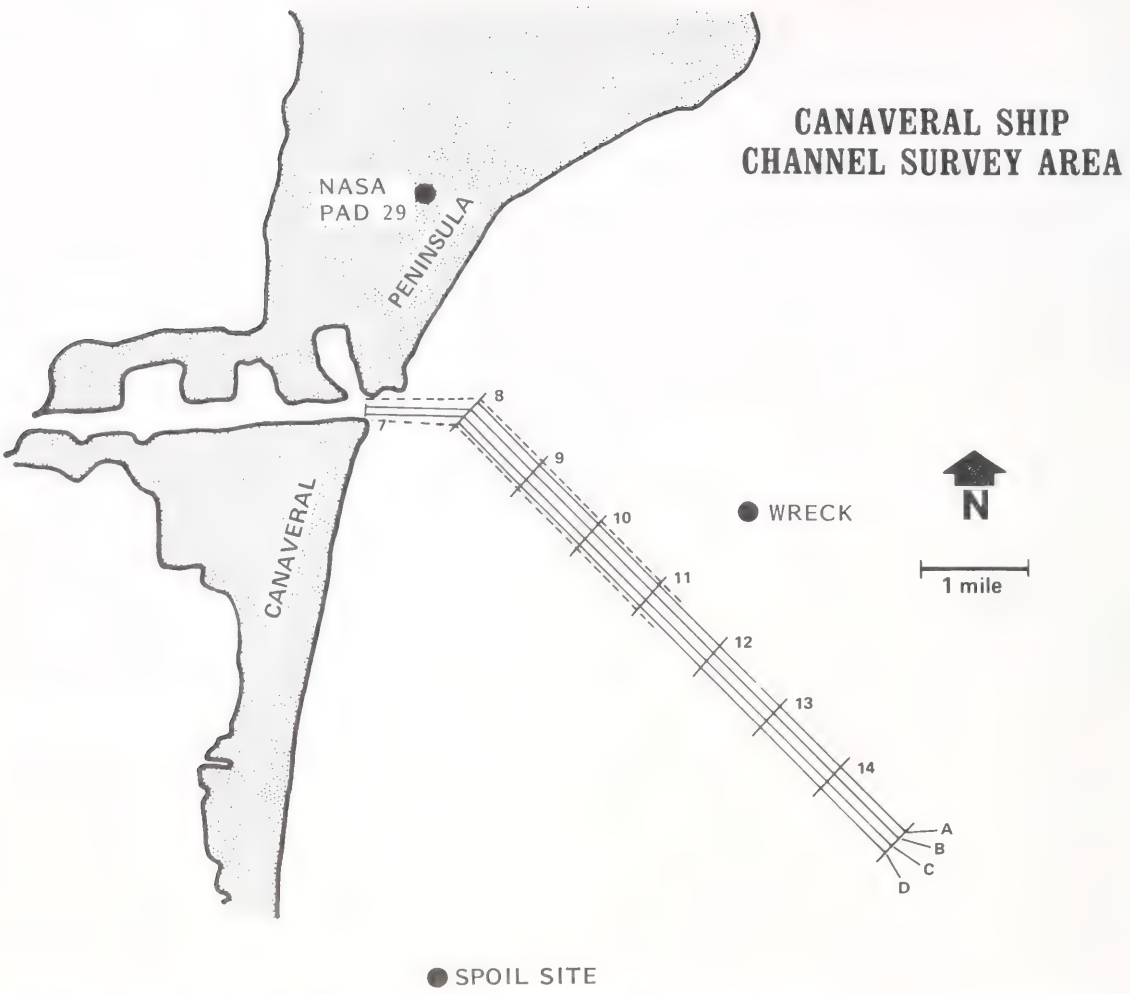

FIGURE 2.—Description of the Port Canaveral ship channel survey area. The channel was separated into 1,483 m stations (7-14), which were divided into 30 m wide substations (A, B, C, and D).

$$\text{Var}\ (\hat{N}_0) = (\text{SE})^2\ [1/n + \overline{X}^2/\Sigma(X_i - \overline{X})^2]$$

where SE = standard error of the estimate provided by the straight line fit
n = sample size of the catch data set
X_i = observed catch per sample in the i^{th} sample and

$$\Sigma(X_i - \overline{X})^2 = \Sigma X_i^2 - \Sigma(X_i)^2/n\,.$$

The estimated variance of P was then calculated using procedures of Mood et al. (1974):

$$\text{Var}\ (\hat{P}) = (C_1/\hat{N}_0^2)^2\ \text{Var}\ \hat{N}_0.$$

In one instance, the experiment was conducted in an area larger than the standard substation and a ratio (standard area/larger area = 0.75) was used as a constant multiplier to standardize estimates.

The mean probability of capture was calculated by combining all experimental P's using the formulae:

$$\hat{\bar{P}} = \hat{P}_i/k, \text{ and Var } (\hat{\bar{P}}) = \text{Var } (\hat{P}_i)/k^2$$

where k = number of estimates.

Once the efficiency of trawling equipment had been determined, the number of loggerhead turtles present in a substation ($\hat{N}$) was estimated using the following formula (Seber 1973):

$$\hat{N} = C/\hat{P}$$

where $\hat{P}$ = probability of capture
C = number of animals captured.

If more than one sample tow was made in a substation, the mean catch ($\overline{C}$) was substituted in the above formula. To estimate the number of loggerhead turtles in a channel substation, station, or the entire channel, the mean number captured per substation sample ($\overline{C}$) times the number of substations (s) was substituted: $\hat{N} = s\overline{C}/\hat{P}$. The estimated variance of this estimate is (Mood et al. 1974):

$$\text{Var}(\hat{N}) = (s/\hat{\bar{P}})^2 [\text{Var}(\overline{C}) + (\overline{C}/\hat{\bar{P}})^2 \text{Var}(\hat{\bar{P}})] .$$

RESULTS

Estimates of the probability of capture and associated standard error estimates from nine repetitive trawl experiments are presented in Table 1. Estimated probability of capture within a substation based on six experiments ranged from 0.21 to 0.31 ($\hat{\bar{P}} = 0.28$; 95% confidence interval = ±0.05; estimated variance = 5.18×10^{-4}). Three experiments were excluded from the analyses: two were discarded because the catch failed to decline due to low population levels, and a third was eliminated because of problems with the sampling trawl.

Estimates of loggerhead turtle abundance by survey for the Port Canaveral ship channel ranged from 701 ± 291 turtles in late February 1982 to a low value of 38 ± 26 turtles in late August 1982 (Table 2). Port Canaveral channel stations 9 through 11 (Fig. 2) exhibited the highest loggerhead turtle abundance during all seasons of the year. Mean catch for all samples in the channel was 2.55 turtles/tow and 0.50 turtles/tow for control samples, supporting the hypothesis that loggerhead turtles congregate in the Port Canaveral ship channel.

Loggerhead turtle abundance estimates for the remaining four survey sites were low during all seasons of the year (Table 3). Over the study period, a total of 18 loggerhead turtles was captured: 2 at St. Mary's entrance, 6 at Ponce de Leon Inlet, 3 at Fort Pierce Inlet, and 7 at St. Lucie Inlet.

DISCUSSION

Our estimates of the probability of capture were based on the supposition that catch-per-tow in a given substation will decrease as loggerhead turtles are removed. The regression of cumulative loggerhead turtle catch on catch per sample can then be used to estimate the orginal population size in the substation (Brownlee 1965) and using this estimate, the probability of capture can be computed. Assumptions associated with this procedure are a closed population, the trawl fishes only within the defined bounds of the substation, each tow is an equal unit of effort and the probability of capture remains constant.

TABLE 1.—Estimated probability of loggerhead turtle capture in a Port Canaveral ship channel substation using an 18 m fish trawl.

Date	Catch on first tow (C_1)	Population estimate (N_0)	Probability of capture ($\hat{P}$)	SE ($\hat{P}$)	Approximate 95% C.I. ($\hat{P}$)
11/6/81	8	20.19	0.40	0.09	±0.17
12/5/81	6	19.54	0.31	0.01	±0.02
12/7/81	13	51.48	0.28	0.03	±0.07
2/28/82	7	30.31	0.23	0.02	±0.04
3/2/82	15	72.85	0.21	0.07	±0.13
5/23/82	2	(*)			
5/28/82	2	(*)			
6/1/82	1	(*)			
8/6/82	3	11.82	0.25	0.05	±0.10
mean ($\hat{P}$)			0.28	0.03	±0.05

[1]Data set discarded.

TABLE 2.—Estimated number of loggerhead turtles ($\hat{N}$) at Port Canaveral ship channel by station and survey period (1981-1982).

Station	Nov. 3-5	Dec. 2-4	Feb. 3-6	Feb. 21-26	May 7-12	May 28-June 1	Aug. 4-5	Aug. 20-22
7	([1])	([1])	[2]0	[2]0	[2]21	[2]0	[2]14	[2]0
8	([1])	([1])	25	43	29	11	21	0
9	93	32	114	143	[2]29	21	57	7
10	64	32	254	221	32	21	61	18
11	21	7	[3]157	146	21	36	8	7
12	21	4	43	89	7	21	4	4
13	0	0	0	11	[2]10	0	0	0
14	0	0	0	4	[2]0	[2]0	0	0
Chanel	[4]200	[4]75	632	701	152	122	168	38
Approx. 95% C.I.	±129	±50	±314	±291	±86	±62	±82	±26

[1]Station not sampled
[2]Station incompletely sampled.
[3]Includes 4 Kemp's ridley turtles, *Lepidochelys kempi*.
[4]Estimate is for stations 9-14, others are for 7-14.

TABLE 3.—Estimated loggerhead turtle abundance during quarterly surveys of St. Mary's entrance—King's Bay, Ponce de Leon Inlet, Ft. Pierce Inlet and St. Lucie Inlet.

Date	St. Mary's King's Bay	Ponce de Leon Inlet	Fort Pierce Inlet	St. Lucie Inlet
11/81	9 ± 18	0	0	0
2/82	0	11 ± 15	4 ± 7	4 ± 7
5/82	0	0	4 ± 8	11 ± 11
8/82	0	0	0	4 ± 7

Although these assumptions may not be satisfied in all cases, our estimates of probability of capture in a given substation were consistent except for the two discarded experiments conducted during periods of low loggerhead turtle densities. These findings suggest that some loggerheads encountering the trawl were able to avoid capture, presumably by moving out of the trawl path. The results also indicate that a consistent percentage of loggerheads were captured by the trawl, facilitating the estimation of turtle abundance based on number of turtles captured. It should be noted that the probability of capture in a given substation (as presented in our results) is lower than the probability of capture in a given tow. To compute the probability of capture in a single tow, the width of the substation is divided by the width of the trawl and this factor multiplied by the probability of capture in the substation.

Loggerhead turtle abundance estimates in the Port Canaveral ship channel exhibited large seasonal variation (Table 2). The estimated population levels during the month of February were significantly higher than all other quarterly surveys indicating that loggerheads were most abundant during winter months. These findings are in agreement with other NMFS surveys in the Canaveral channel from 1978 to 1983 (Table 4) and support the contention of Carr et al. (1980) that loggerhead turtles may hibernate in the Port Canaveral channel in refuge from low water temperatures. The fact that the winter of 1981-82 was unusually mild, could account for the lack of an early winter peak in loggerhead turtle abundance observed in previous years.

Data presented in Table 4, while of limited statistical value due to inconsistencies in sampling methodologies, are useful for comparisons between this study and other NMFS Canaveral channel surveys. It is worthy of note that mean catch per unit effort (CPUE) by month combining all years was in excess of 10 loggerhead turtles/hour from November through March with peak concentrations in February and March. Lowest CPUE values and presumably population levels occurred from April through September, which is in agreement with our findings.

It is evident that loggerhead turtle abundance estimates were highly variable between surveys made in the same quarter (Table 2). We speculate that these fluctuations in population levels were caused by short-term immigration and emigration in response to local weather changes. We have observed daily changes in catch rates which appear to be correlated with passage of weather fronts.

Distribution of loggerhead turtles within the Port Canaveral ship channel is also of interest. In every survey, stations 9, 10, and 11 exhibited the highest abundances, suggesting that they were preferred turtle habitat. Stations 7, 8, and 12 exhibited intermediate population levels and stations 13 and 14 had low turtle abundance levels. Stations 7, 8, 9, and 10 were those where deepest cuts into the seabed have been made by dredging. The bottom was characterized by divers as clay-silt and detritus as opposed to the harder clay-sand bottom outside the channel (Carr et al. 1980).

Interpretation of loggerhead turtle abundance estimates generated from this study is complicated by the fact that three different groups of

TABLE 4.—Summary of catch per unit effort (CPUE) of loggerhead turtles in the Port Canaveral ship channel (1978-83). Values are in turtles per hour standardized to a single 100-ft net. N = number of tows.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1978		37.74 $N = 7$	55.73 $N = 7$							18.99 $N = 5$	10.82 $N = 10$	21.64 $N = 14$
1979	11.56 $N = 17$	11.88 $N = 11$	8.21 $N = 11$	9.13 $N = 3$	1.33 $N = 5$	21.25 $N = 16$	13.86 $N = 32$		9.43 $N = 28$			
1980	24.82 $N = 19$	19.61 $N = 40$	28.57 $N = 77$		3.38 $N = 22$	3.77 $N = 22$	3.31 $N = 60$	3.29 $N = 152$	2.62 $N = 189$	5.44 $N = 135$	11.81 $N = 105$	5.11 $N = 7$
1981		15.89 $N = 12$		11.22 $N = 16$				7.88 $N = 41$	3.26 $N = 51$		22.06 $N = 29$	7.18 $N = 42$
1982		41.83 $N = 99$	58.53 $N = 14$		7.49 $N = 96$	4.24 $N = 15$		5.95 $N = 83$				
1983			4.86 $N = 20$	2.35 $N = 60$								
Totals	18.56 $N = 36$	32.61 $N = 169$	27.88 $N = 129$	4.21 $N = 79$	6.50 $N = 123$	9.18 $N = 53$	6.98 $N = 92$	4.77 $N = 276$	3.45 $N = 268$	5.92 $N = 140$	13.80 $N = 144$	10.16 $N = 63$

loggerheads (adult males, adult females, and subadults) utilize the channel at different times of the year (Henwood 1987). Adult males are dominant in April and May, adult females are most abundant from May through August and subadult turtles are predominant during the remainder of the year. For this reason, direct comparisons between quarterly surveys may be inappropriate.

It is unfortunate that the three discarded repetitive trawl experiments occurred in May and June when the population was comprised primarily of breeding adults. Low population levels at this time may reflect a reduced catchability coefficient in adult loggerhead turtles possibly associated with behavioral changes. The ability of loggerhead turtles to escape trawls may also be enhanced during periods of high water temperatures, but no evidence of this was noted during August or November.

Loggerhead turtle abundance in the remaining four channels was low during all quarterly surveys. These findings confirm the presence of loggerhead turtles along much of Florida's eastern coastline, but do not indicate any channel areas with turtle concentrations similar to Port Canaveral. It is of special interest that only Port Canaveral, a manmade habitat, harbors concentrations of loggerhead turtles throughout the year and particularly during winter months.

The St. Mary's entrance to King's Bay survey area was by far the largest site investigated and may have been incompletely sampled relative to the total area involved. This location was of particular interest to the U.S. Navy because of planned construction of a Trident submarine base in King's Bay. Although no concentrations of loggerhead turtles were noted over the course of this investigation, future dredging of this channel could potentially result in a situation similar to Port Canaveral, with loggerhead turtles congregating in a deepwater manmade habitat.

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HOMING MIGRATION OF SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, TO THE FRASER RIVER

C. GROOT[1] AND T. P. QUINN[2]

ABSTRACT

Adult sockeye salmon, *Oncorhynchus nerka,* return to the Fraser River via either of two routes: a northern route through Queen Charlotte Strait, Johnstone Strait, and the Strait of Georgia between the mainland and Vancouver Island, and a southern route along the west coast of Vancouver Island and through Juan de Fuca Strait. The proportions of the total run of sockeye salmon using the two routes varies substantially from year to year. Understanding the factors influencing the migratory routes of Fraser River sockeye salmon provides a basis for forecasting the coastal migrations of salmon as they make the transition between oceanic and riverine environments. Our analysis of west coast troll catch and high seas tag-recovery data indicates that the salmon make landfall in different coastal regions from year to year. If the majority of Fraser sockeye approach the coast of Vancouver Island, then most will migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait. Northern diversion rates of Fraser River sockeye salmon for the period 1953-77 were positively correlated with Fraser River discharge. For the period 1978-85 a strong positive correlation was evident with sea surface temperature (SST) along the northwest coast of Vancouver Island (Kains Island lighthouse). We conclude that Fraser River discharge and SST in the vicinity of Kains Island do not guide sockeye salmon in any direct way during their coastal approach, but that they reflect oceanographic conditions that affect salmon migrations directly or indirectly by acting on the feeding distribution, distance, or direction they must travel to reach home.

The Fraser River in British Columbia, Canada, is among the most important producers of sockeye salmon, *Oncorhynchus nerka*, in North America. Forty to sixty separate stocks, inhabiting the different lakes of its watershed, produce 2 to 20 million adults yearly (IPSFC 1954-1985). Sockeye salmon from the Fraser River system generally spend 1 year in nursery lakes after emergence and then migrate to sea as smolts. Most spend two winters in the ocean, returning to spawn in their home river as 4-yr-olds. To reach the Fraser River from their ocean feeding grounds they can take either of two routes around Vancouver Island (Fig. 1). From 1953 until 1977, the majority homed via the southern route through the Strait of Juan de Fuca (average 84%, range 65-98%). Since 1978, a larger proportion of sockeye have migrated via the northern route through Johnstone Strait (average through Juan de Fuca Strait 56%, range 20-78%) (IPSFC 1954-1986).

In 1958 a relatively high proportion (35%) of Fraser River sockeye salmon returned via the northern route. A large number of fish did not make landfall off the west coast of Vancouver Island but rather arrived in the more northerly Queen Charlotte Sound area (Tully et al. 1960) (Fig. 1). This coincided with anomalously high water temperatures off the coast of British Columbia. Tully et al. (1960) and Royal and Tully (1961) suggested that intrusion of warm water from the south in 1958 directed the homing sockeye salmon northward and closer to the mainland. Moreover, the fish appeared 10 days later in the fishery around Vancouver Island and over a longer period than usual, suggesting that they might have detoured around the area of warm water and made their coastal approach in the cooler nearshore waters. Alternatively, they might have initiated their homeward migration later or from a more distant area than usual.

Favorite (1961), on the other hand, took the view that the unusual extent of dilute seawater of Fraser River origin offshore from Queen Charlotte Sound in 1958 determined the location where the migrating sockeye entered coastal water. He assumed that homeward migrating salmon are attracted to dilute seawater contain-

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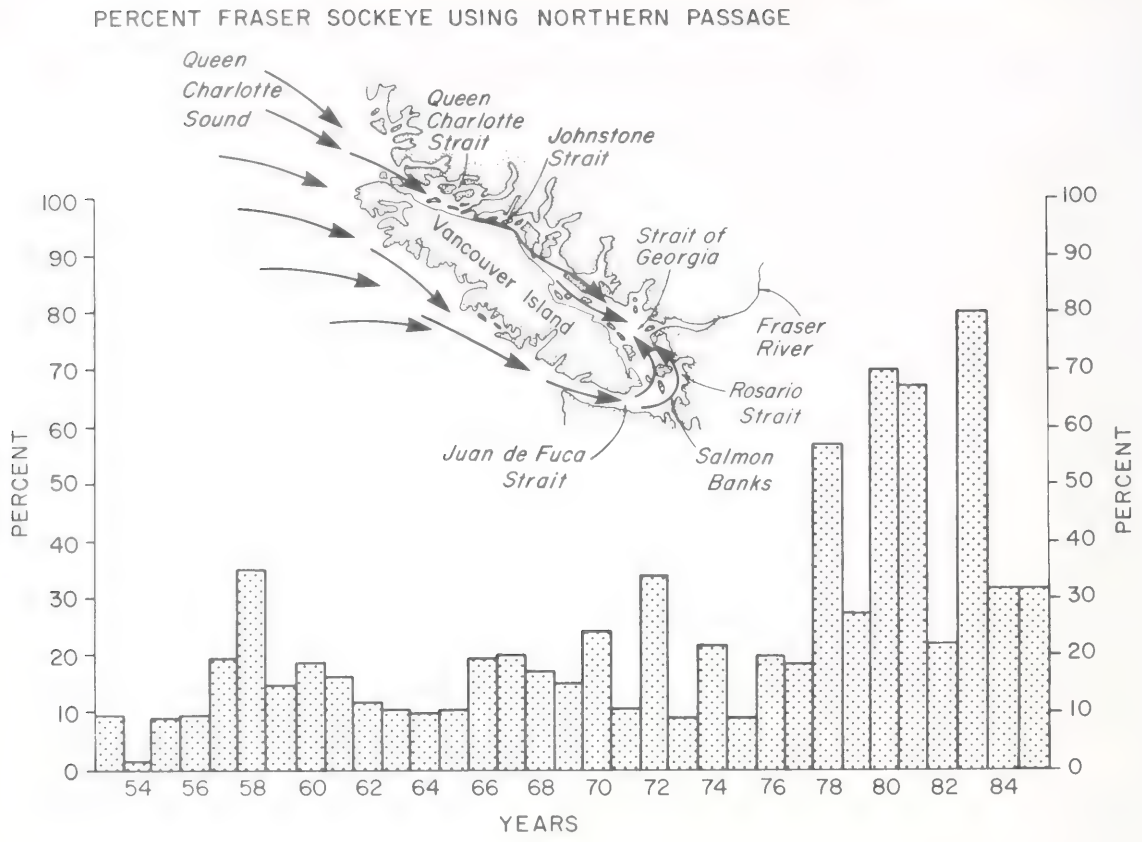


FIGURE 1.—Migratory routes of adult sockeye salmon returning to the Fraser River around Vancouver Island. The bar graph indicates the proportion of the total run that was estimated to have used the northern route (data from IPSFC annual reports).

ing homestream odors. Wickett (1977) extended this hypothesis by using indices of oceanographic processes to indicate the extent of dilute water plumes off Queen Charlotte Sound from 1953 to 1976. He concluded that the large proportion of Fraser River water discharged into the ocean northwest of Vancouver Island increased the rate of Fraser sockeye migrating through Johnstone Strait. The assumptions by Favorite (1961) and Wickett (1977) were influenced by the proposal of Hasler and Wisby (1951) that riverine odors learned during sensitive juvenile stages guide the homeward migration of adults in nearshore and river environments (Hasler 1966; Hasler and Scholz 1983).

We evaluated the extent to which oceanographic conditions in offshore waters influence the migratory routes of returning Fraser River sockeye around Vancouver Island. Nine more years of data (1977-85) have become available since Wickett's (1977) publication and four of these show unprecedented (57% to 80%) diversion rates via Johnstone Strait.

COASTAL MIGRATORY PATHWAYS OF FRASER RIVER SOCKEYE

INPFC Data

Under the auspices of the International North Pacific Fisheries Commission, Canada, the United States and Japan tagged 99,576 sockeye salmon in the North Pacific Ocean east of long. 165°E between 1956 and 1983. Of these, 4,842 were recovered, mostly (99.4%) along the coast of British Columbia and Alaska (INPFC 1984). We isolated data on Fraser River sockeye salmon from this larger data set to determine the migratory routes of these salmon. In the waters around Vancouver Island, 745 sockeye salmon were recovered. Since sockeye salmon home accurately (Ricker 1972; Foerster 1968; Quinn 1985), the

high seas tagging locations of the recovered fish give information on the distribution of Fraser River sockeye in the ocean. Southern British Columbia sockeye (of which at least 90% are Fraser River fish) were distributed in the Gulf of Alaska southward to lat. 45°N and westward to long. 178°E, a distance of 6,600 km from the Fraser River. The monthly changes in distribution of tagged fish from April to August and recovered in the year of tagging suggest that during spring and summer there is first a shift northeastward in May and June and then southeastward in July and August along southeast Alaska and the Queen Charlotte Islands towards Vancouver Island (Fig. 2). The findings are in accordance with the migration model for southeast British Columbia sockeye salmon presented by French et al. (1976).

Further indications of the coastal approach routes of Fraser River sockeye salmon can be derived from the rate of travel and the assumed direction of movement. From the positions and the dates of tagging and recovery, the rate of travel along the shortest route can be calculated for each fish. The rates ranged up to 98 km/day (4.1 km/hour or about 2 body lengths/second). Sonic tracking studies by Madison et al. (1972), Stasko et al. (1976), and Quinn and terHart (in press) showed that sockeye salmon travel at average speeds of 1.8 to 2.2 km/hour (about 1 body length/second) when migrating, which approximates the optimum sustained swimming speed for mature sockeye in endurance tests (Brett 1983).

For 373 sockeye salmon that were tagged 1,000 km or more away from the Fraser River and recovered around Vancouver Island, 86 (or 23%) travelled at speeds greater than 45 km/day (1.9 km/hour or about 1 body length/second) (Fig. 3). These estimates of swimming speed discount any effect of currents. Current direction and speed vary considerably in the regions through which

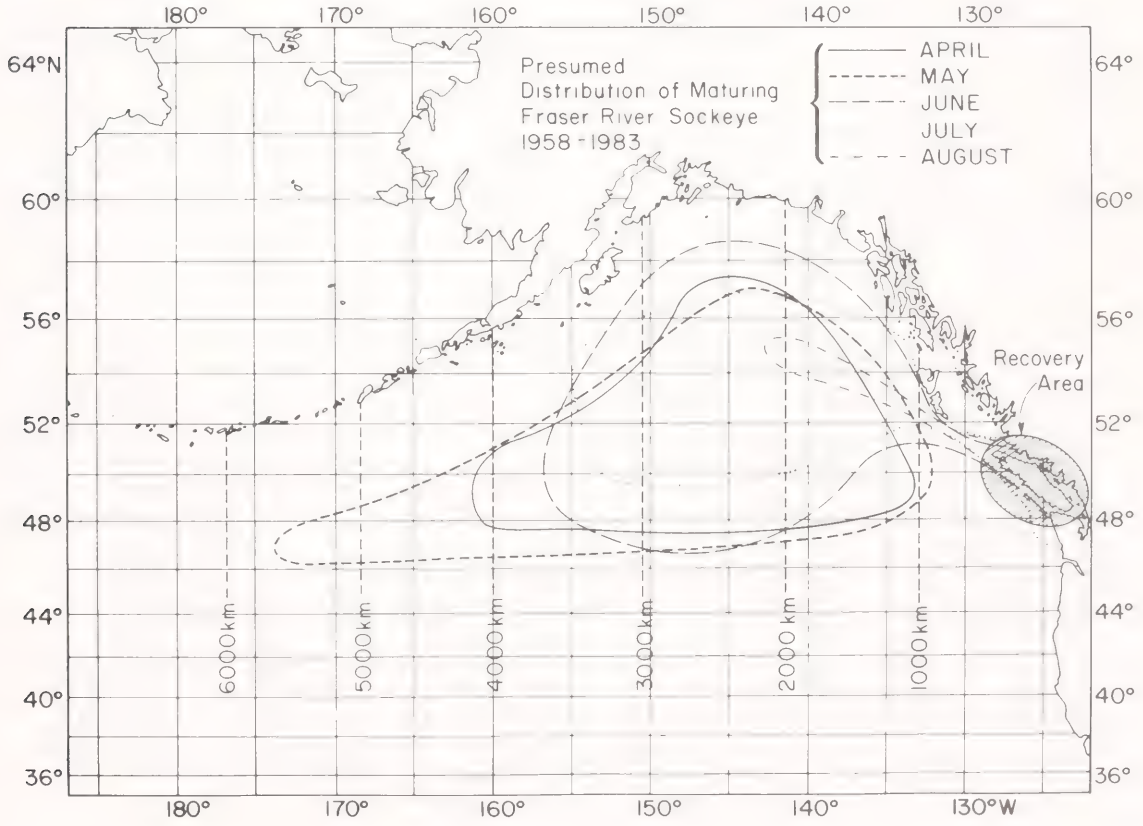


FIGURE 2.—Distributions in the Gulf of Alaska of releases of sockeye salmon from April through August that were recovered during the year of tagging around Vancouver Island, 1953-85.

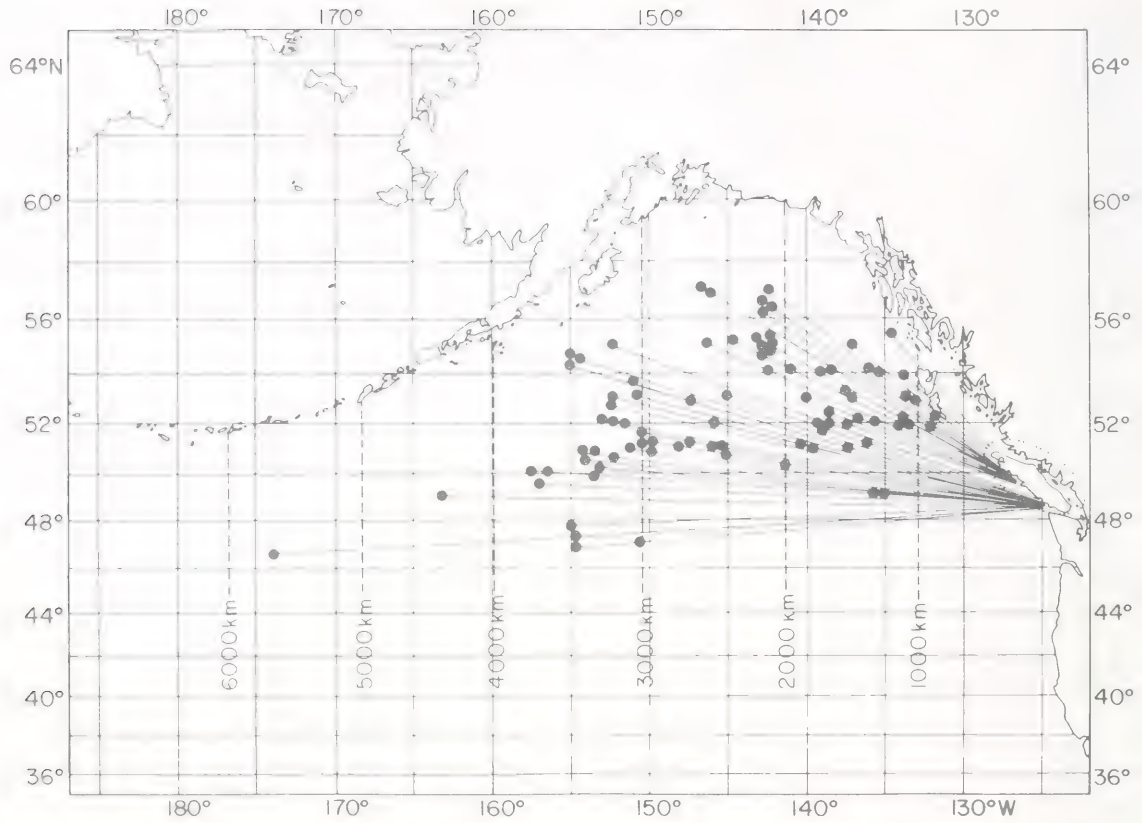


FIGURE 3.—Locations where maturing sockeye salmon were tagged and recovered in the Vancouver Island area. Only recoveries farther than 1,000 km away from the entrance of the Fraser River and with speeds over 45 km/day are illustrated.

the sockeye migrate but are usually less than 0.4 km/hour (Favorite et al. 1976; Tabata 1984). We assume that these fish must have travelled on relatively direct courses, day and night, based on the optimum speed of sockeye salmon (~2 km/hour) and the fact that substantial divergence from straight-line travel would have required the salmon to exceed their fatigue speed of 5 km/hour to accomplish the observed displacements (Quinn 1984; Quinn and Groot 1984). Connecting the tagging positions of these 86 sockeye salmon with the mouth of the home river shows that they must have approached Vancouver Island from a westerly or northwesterly direction (Fig. 3). The sockeye salmon that were about 3,000 km or more from the Fraser River (mostly tagged in April and May) were generally distributed farther to the south than those tagged later in the season at distances from 1,000 to 2,300 km. The former must have travelled almost due east, while most of the latter may have moved northeast first and then later in the season turned southeast towards Vancouver Island.

Thus, sockeye salmon returning to the Fraser River from their ocean feeding grounds approach Vancouver Island from the west and the northwest and, depending on their homing course, generally make landfall along the west coast of Vancouver Island or farther north in Queen Charlotte Sound (Fig. 1).

West Coast Troll Fishery

To derive information on areas of landfall for different years, we used records of troll fishing off the west coast of Vancouver Island. The Canadian west coast fishery has usually been open during the period that sockeye salmon arrive on the coast. Only during 1978, 1982, 1983, and 1985 were there short nonretention periods for sockeye salmon. We assume, therefore, that in general the catches reflect the migratory patterns of these

fish in nearshore waters. The troll catches and boat efforts are recorded on a weekly basis for the different statistical areas by the Department of Fisheries and Oceans of Canada (F. Wong[3]). The west coast sockeye salmon catches generally reflect the annual variability in the total Fraser River run (Henry 1961); therefore, most sockeye salmon captured along the west coast are considered to be returning to this river. Small proportions of the catch are of Barkley Sound (Vancouver Island) and Lake Washington (USA) origin.

In 1979 and 1982 peak catches of sockeye salmon occurred near the middle of Vancouver Island in areas 24-26 (Fig. 4). The relatively low diversion rates (27 and 22% respectively during

[3]F. Wong, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

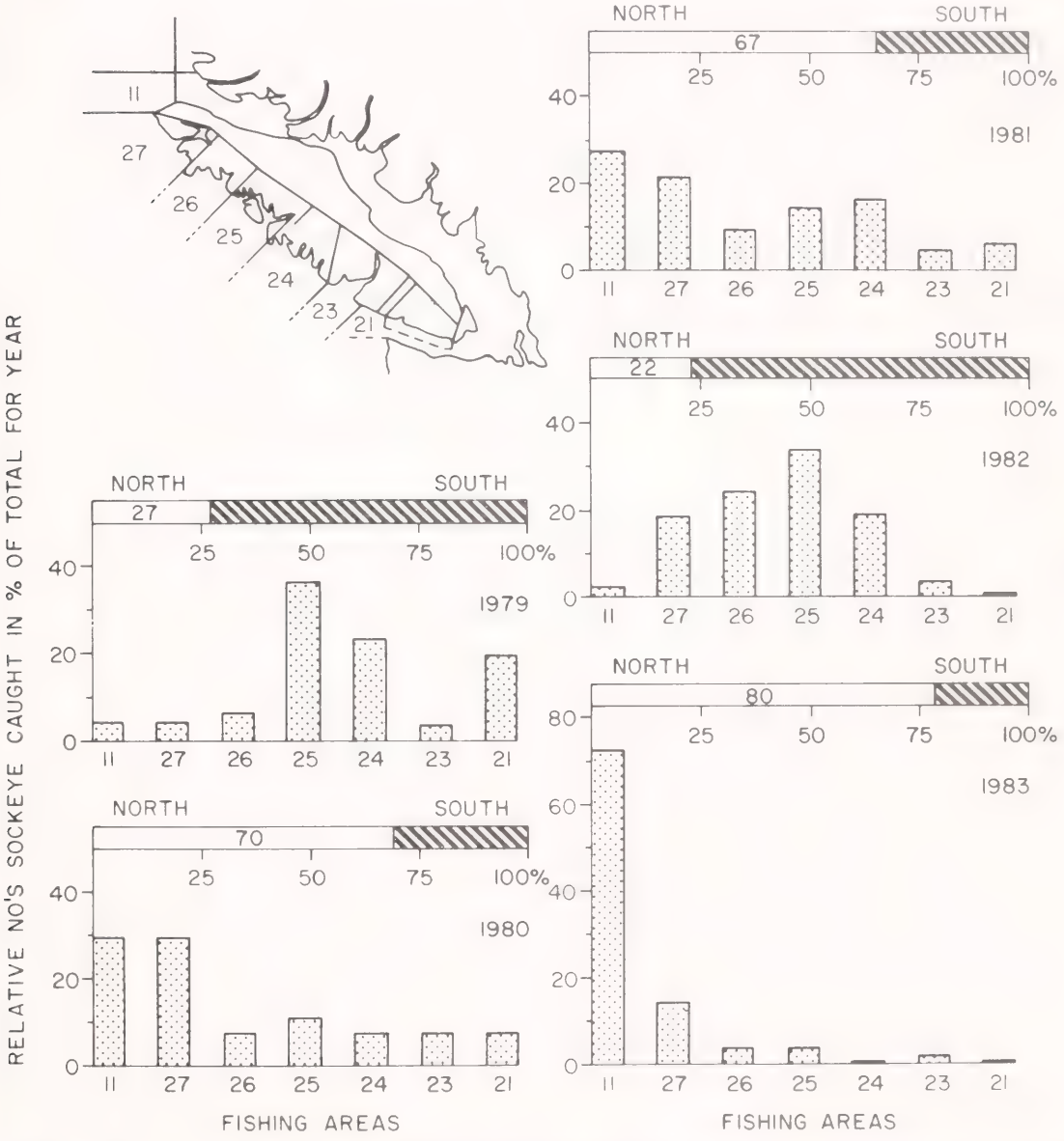


FIGURE 4.—Vertical bar graphs illustrate the proportions of the total troll catch of sockeye salmon off the west coast of Vancouver Island caught in different statistical areas (see map insert) for the years 1979-83. Horizontal bars indicate the proportions of sockeye salmon migrating to the Fraser River via the northern and southern routes.

these years) indicate that most sockeye may have migrated southwest from a relatively southerly position offshore and returned to the Fraser River via the Strait of Juan de Fuca. In 1980 and 1981 the largest sockeye catches were made near the north of Vancouver Island in areas 11 and 27 (Fig. 4). In these years 70 and 67% of the Fraser sockeye migrated through Johnstone Strait. In 1983 an extreme situation prevailed: most of the sockeye salmon were caught in area 11 (Queen Charlotte Sound) and 80% of the fish migrated via the northern route (Fig. 4).

From these results we conclude that the proportions of Fraser River sockeye salmon returning via the northern and southern routes are generally associated with the area where the fish make their landfall (see also Tully et al. 1960; Henry 1961; IPSFC 1979-1984). If the majority of Fraser sockeye approach the coast west of Vancouver Island, then most will continue to migrate via the Strait of Juan de Fuca. However, when landfall occurs north of Vancouver Island in the Queen Charlotte Sound area, most homeward migrating Fraser sockeye will travel through Johnstone Strait.

North Coast Salmon Tagging Project

During 1982 and 1983, Canada and the United States tagged sockeye salmon along the coast of northern British Columbia and southeastern Alaska to determine interception rates in the commercial fisheries of both countries near the boundary. The results of these studies provide additional information on migratory routes of this species along the North American coast. In 1982, 40,556 and in 1983, 23,052 maturing sockeye salmon were tagged in several places in southeastern Alaska and northern British Columbia (Fig. 5) (B. Riddell[4]). Most of these fish were heading for spawning rivers in southeastern Alaska and the Nass and Skeena Rivers of northern British Columbia. However, a number of sockeye salmon, 24 in 1982 and 126 in 1983, were recovered in the commercial fishery around Vancouver Island. We assume that most of these were Fraser River fish because more than 90% of sockeye salmon captured in southern British Columbia belong to Fraser River stocks.

Of the sockeye salmon tagged in the north, 9 times more were recovered in the Vancouver Island area in 1983 than in 1982 (Fig. 5), despite the fact that the total run of sockeye to the Fraser River in 1982 (13,933,000) was more than twice as large as in 1983 (5,167,000; IPSFC 1983, 1984). This indicates that in 1983 a greater proportion of Fraser River sockeye made landfall north of Vancouver Island than in 1982. This was reflected in the diversion rates through Johnstone Strait of 80 and 22% respectively for the 2 years (Figs. 1, 4). The results also show that relatively 9 (1982) to 13 (1983) times more sockeye were recovered in the Vancouver Island area from the outside (Noyes and Queen Charlotte Islands, and Cape Muzon) than from the inside (Clarence Strait and Areas 3, 4, and 5) tagging operations (Fig. 5). We suggest that the southern British Columbia sockeye primarily migrated along the west coast of the Queen Charlotte Islands during their migration south. However, some entered Dixon Entrance in 1983 and travelled through Hecate Strait towards the Fraser River, as indicated by recoveries from inside tagging locations.

The findings from the North Coast Tagging Project support the evidence presented earlier that coastal migratory routes of Fraser River sockeye can vary considerably from year to year and that during years of high diversion through Johnstone Strait the returning sockeye make landfall farther north. Analysis of catches, run timing, and stock composition led the Pacific Salmon Commission to a similar conclusion several years ago (IPSFC 1983).

In summary, our analysis of the INPFC, West Coast Troll, and North Coast Tagging data sets indicates that Fraser River sockeye salmon returning from ocean feeding grounds approach Vancouver Island from the west and northwest. The area of landfall varies yearly from the west coast of Vancouver Island to more northern regions in Queen Charlotte Sound. Moreover, the area where most salmon reach the coast is strongly correlated with the proportion that enters the Strait of Georgia via the southern or northern routes.

Migratory Routes and Oceanographic Conditions

A coastal approach north of Vancouver Island results in a higher proportion of fish moving through Johnstone Strait, while an approach farther south, along the west coast of Vancouver Island, directs the fish to the Fraser River through

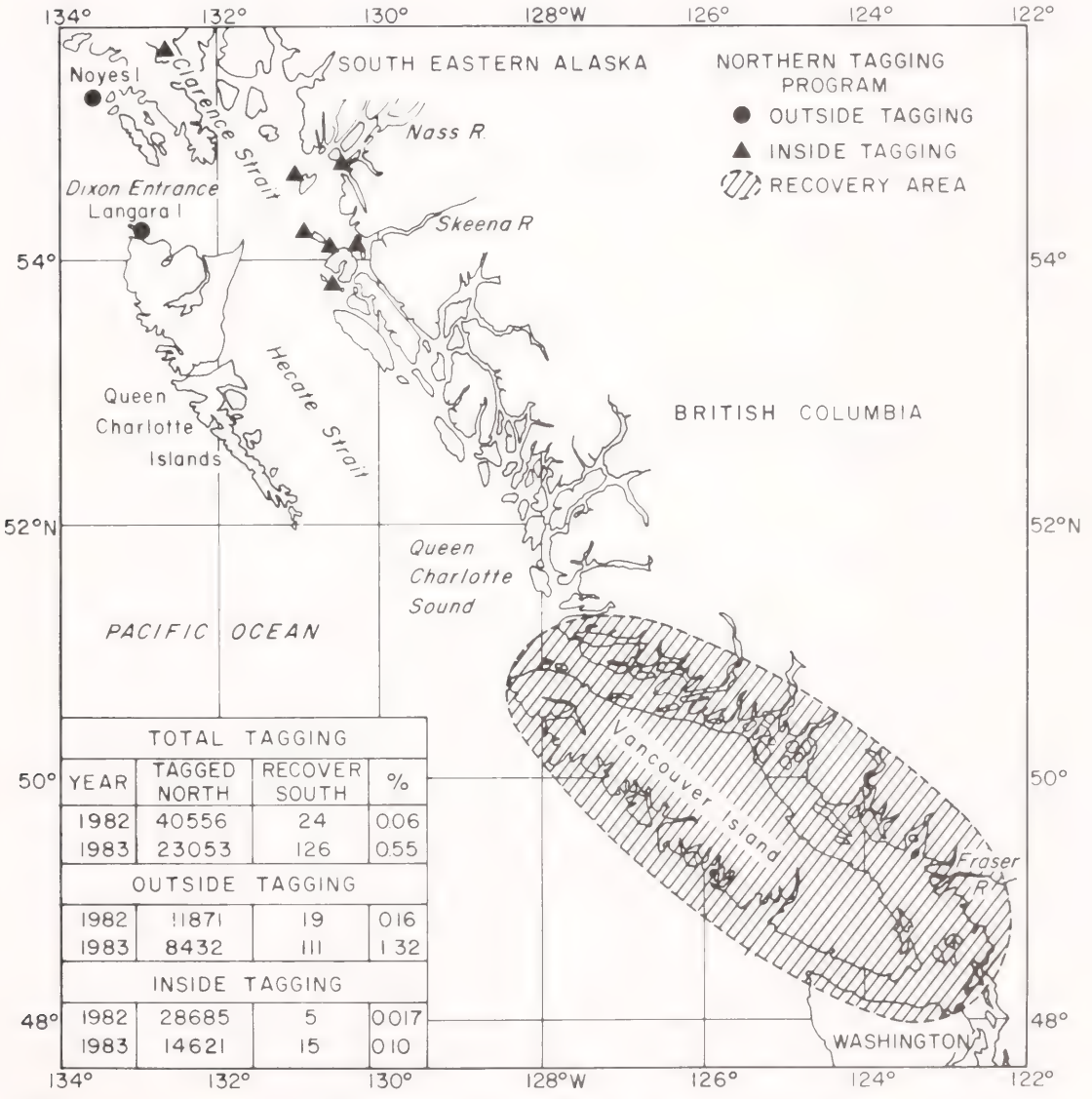
[4]B. Riddell, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1985.

the Strait of Juan de Fuca. We propose that the coastal approach may be influenced by oceanographic conditions in the eastern Gulf of Alaska during the April-June period when the maturing sockeye perform their homing migrations from the high seas overwintering grounds to the coastal areas (French et al. 1976).

The following environmental factors were analyzed for correlation with diversion rates of Fraser River sockeye via the north:

1) Sea surface temperatures (SST) (average April-June) measured daily at four lighthouse stations along the British Columbia coast: Amphitrite Point, Kains Island, Cape Saint James, and Langara Island (Fig. 6) (Dodimead 1984; L. F. Giovando[5]). SSTs can be used as indications

[5]L. F. Giovando, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.



TOTAL TAGGING			
YEAR	TAGGED NORTH	RECOVER SOUTH	%
1982	40556	24	0.06
1983	23053	126	0.55
OUTSIDE TAGGING			
1982	11871	19	0.16
1983	8432	111	1.32
INSIDE TAGGING			
1982	28685	5	0.017
1983	14621	15	0.10

FIGURE 5.—The numbers of sockeye salmon tagged in northern British Columbia and southeastern Alaska and recovered that year in waters around Vancouver Island. Tagging data are separated by location of tagging (inside vs. outside waters) and year (1982 vs. 1983).

FIGURE 6.—Locations where environmental conditions were monitored for regression analysis with sockeye salmon migratory patterns: sea surface temperature and salinity at Amphitrite Point, Kains Island, Cape St. James, and Langara Island; sea level at Tofino; Ekman transport at lat. 51°N, long. 131°W; and Fraser River discharge at Hope.

of the extent of warm water intrusion from the south along the coast.

2) Sea surface temperatures (average April-June) at ocean station P (50°N, 145°W) (see Figure 8) (S. Tabata[6]) as an indication of ocean conditions in the Gulf of Alaska. After sampling at this station was terminated in 1981, temperatures for this area in the Pacific Ocean were obtained from satellite and shipboard observations.

3) Monthly mean sea-levels (average April-June) recorded at Tofino, on the west coast of Vancouver Island (Fig. 6), as an indication of convergent and divergent conditions along the coast (A. Dodimead[7]). Also, high coastal sea levels indicate northward currents.

4) Ekman transport normal to the coast (average April-June) at 51°N, 131°W (Fig. 6) calculated from barometric pressure data (Dodimead 1984; Giovando fn. 5) to indicate the general pattern of circulation from wind-driven transport.

5) Fraser River discharge (average April-June) measured at Hope (Fig. 6) (LeBlond et al. 1983; Inland Waters Directorate[8]), as an indication of coastal run-off and extent of Fraser River homewater along nearshore areas.

Linear regression analysis of Fraser sockeye diversion rates from 1953 to 1985 with SST of lighthouse data from Amphitrite Point, Kains Island, Cape St. James, and Langara Island for the months of April to June showed significant correlations (Table 1). Since the correlation coefficient of diversion rates was highest with the data from the Kains Island lighthouse, these were selected for further analysis and averaged over April, May, and June.

Regression analysis between the northern diversion rates and the environmental variables

[6]S. Tabata, Institute of Ocean Sciences, Patricia Bay, B.C. V8L 4B2, Canada, pers. commun. 1985.

[7]A. Dodimead, Pacific Biological Station, Nanaimo, B.C. V9R 5K6, Canada, pers. commun. 1984.

[8]Inland Waters Directorate, 1001 West Pender Street, Vancouver, B.C. V6E 2M9, Canada, 1985.

TABLE 1.—Correlations (R) of sea surface temperature at four lighthouse stations along the British Columbia coast with the percentage of sockeye salmon returning to the Fraser River via Johnstone Strait during the years 1953-83.

Lighthouse stations	March		April		May		June	
	R	*N*	R	*N*	R	*N*	R	*N*
Amphitrite Pt.	0.65	31	0.69	31	0.59	31	0.59	31
Kains Island	0.65	31	0.65	31	0.65	31	0.63	31
Cape St. James	0.54	30	0.68	29	0.66	30	0.54	30
Langara Island	0.55	31	0.62	31	0.65	31	0.64	29

listed above for the years 1953-85 showed significant ($P < 0.01$) positive correlations with nearshore (Kains Island) SSTs, explaining 51% of the variance (Table 2; Fig. 7A).

TABLE 2.—Relationship (R and R^2) for linear regression analyses of average April-June SST at Kains Island lighthouse, sea level at Tofino, Ekman transport at lat. 50°N, long. 131°W, SST at Station P (50°N, 145°W), and Fraser River discharge at Hope with percentage sockeye salmon returning to the Fraser River via Johnstone Strait for the years 1953-85 ($N = 33$), 1953-77 ($N = 25$), and 1978-85 ($N = 8$). The level of significance was set at $P < 0.01$.

Factors	1953-85		1953-77		1978-85	
	R^2 (%)	R	R^2 (%)	R	R^2 (%)	R
SST Kains Island	51	0.71*	9	0.30	85	0.92*
Sea level Tofino		0.19	19	0.44	3.9	0.20
Ekman transport	4	0.29	4	−0.20	5	0.23
SST Station P	15	0.39	11	0.33	11	0.33
Fraser River discharge	2	0.14	45	0.67*	30	−0.55

*$P < 0.01$.

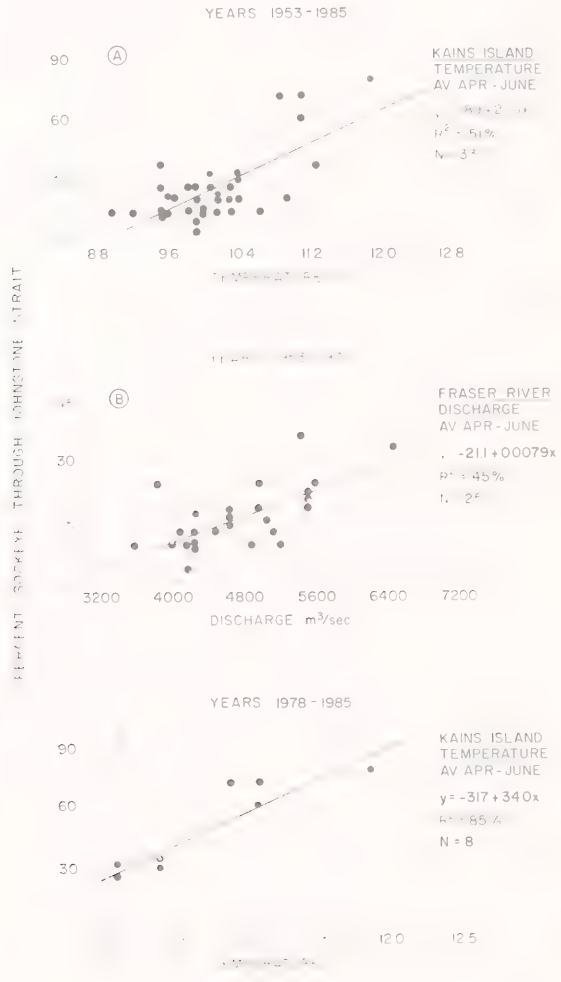


FIGURE 7.—Relationships between the proportion of Fraser River sockeye salmon migrating via the northern route (Johnstone Strait) and A) average sea surface temperature and salinity at Kains Island for April, May, and June for the years 1953-85; B) average Fraser River discharge for April, May, and June for the years 1953-77; C) average sea surface temperature at Kains Island for April, May, and June for the years 1978-85.

Inspection of the diversion rates over the last 33 years suggested that after 1977 a change occurred in the migratory patterns of Fraser River sockeye approaching the coast. During the period 1978-85, unprecedented rates of 70 to 80% have used the northern route (Fig. 1). This change in migratory behavior coincided with a remarkable prolonged warming period in the northeast Pacific Ocean (Chelton 1984; McClean 1984). The trend culminated in the extended warm-water anomaly of 1983 along the coast of British Columbia, which was associated with the 1982-83 El Niño event that occurred in the equatorial Pacific Ocean. This event was one of the most extreme of the century (Mysak 1985). We therefore carried out separate analyses for the two periods, 1953-77 and 1978-85.

The regression analyses for the 1953-77 period identified Fraser River discharge as the only significant ($P < 0.01$) factor, explaining 45% of the variance (Table 2; Fig. 7B). This positive relationship between northern diversion rates and Fraser River discharge was also suggested by Wickett (1977) for the same time period.

For the period 1978-85, the regression analyses indicated that SST at Kains Island was the only helpful predictor, explaining 85% of the variance (Table 2; Fig. 7C). A strong positive relationship between northern diversion rates of Fraser River sockeye salmon and SST at Kains Island was also noted for the years 1973-83 by staff of the Pacific Salmon Commission (IPSFC 1984).

DISCUSSION

We suggest that sockeye salmon returning to the Fraser River may have been influenced by year-to-year changes in ocean conditions during and between the periods 1953-77 and 1978-85. The relationships of sockeye migration to sea surface temperature and river discharge will be discussed separately.

Sea Surface Temperature and Sockeye Salmon Migration

Leggett's (1977) review of fish migration concluded that oceanic fish migrations largely represent the continuous optimization of physiologically important conditions. Temperature is an oceanographic feature whose importance in fish physiology is well established (Brett 1970). While evidence indicates that thermal conditions may be correlated with the timing of salmon migrations (Burgner 1980; Blackbourn in press) or the route of their return migration to coastal waters (this study), it is not clear how temperature affects salmon behavior. Temperature might directly influence salmon in some way or it might merely correlate with some other oceanographic feature influencing them such as eddies and currents (Mysak 1986), or the abundance or species composition of prey items (Fulton and LeBrasseur 1985). If so, a correlation of salmon behavior with temperature could mislead attempts to understand the control of migration.

Alternatively, temperature may indeed have a direct impact on sockeye salmon. There is considerable evidence that temperature is correlated with the distribution of marine fishes (Brett 1970; Laurs and Lynn 1977; Laurs et al. 1977; Magnuson et al. 1980). Manzer et al. (1965) and French et al. (1976) summarized the distribution of sockeye salmon in relation to sea surface temperature. While waters of certain temperatures were generally devoid of sockeye salmon, the apparent thermal preferendum was 3° to 5°C wide and changed seasonally. Manzer et al. (1965) reported that most sockeye were caught by research gill nets in the North Pacific Ocean and Bering Sea in waters of 4° to 6°C in May, 4° to 7°C in June, 8° to 12°C in July, and 9° to 12°C in August. Based on the occurrence of sockeye salmon in large areas of the North Pacific Ocean, French and Bakkala (1974) concluded that they are not exclusively associated with specific oceanic conditions.

To determine the ways in which temperature might directly affect sockeye salmon, we must ascertain the horizontal and vertical distribution of temperatures which they experience at sea on their homeward journey. An oceanographic survey of the North Pacific Ocean and Gulf of Alaska from 16 to 24 July 1959 (S.I.O.U.C. 1965) provide useful data to suit this purpose (Fig. 8). Temperatures at 0, 30, and 50 m depth were used to estimate the extent of horizontal and vertical gradients experienced by salmon migrating to the northern tip of Vancouver Island along the path which Fraser River sockeye seem to take.

If we assume that salmon swam 48 km/day on the surface along the route of the ship, they would have experienced total temperature changes of +3.68°C or a daily average of +0.10°C/day (Table 3). Averaged over the stations, vertical excursions from 0 to 30 m would have caused the fish to experience changes of −0.81°C. Dives from the surface to 50 m would have been accompanied by changes averaging −5.00°C. Earlier in the sum-

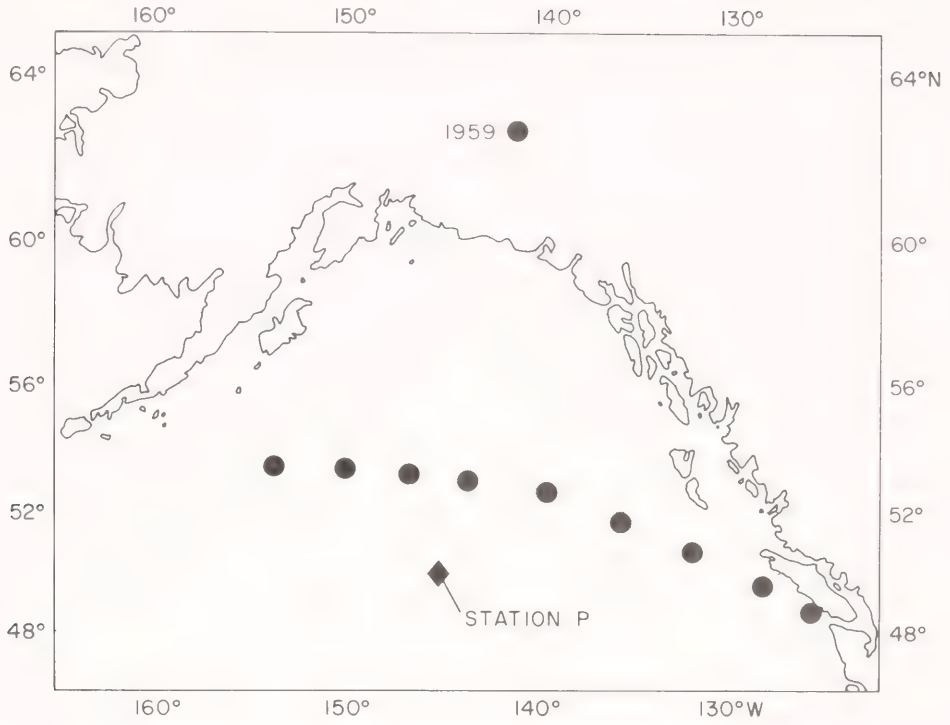


FIGURE 8.—Map of the North Pacific Ocean showing the sites sampled by an oceanographic cruise in 1959 (S.I.O.U.C. 1965) and Station P, where sea surface temperatures and salinities were also recorded.

TABLE 3.—Temperature at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965).

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	10.52	9.98	4.80
53°42′	149°43′	10.54	9.49	4.60
53°30′	146°42′	10.82	9.94	4.80
52°58′	143°27′	11.20	10.90	6.82
52°18′	139°35′	10.90	10.70	6.79
51°40′	135°55′	12.39	12.12	8.58
50°40′	131°57′	13.59	10.60	8.18
49°30′	128°12′	14.20	13.96	9.59
48°44′	125°39′	[1]13.18	[1]8.90	[1]8.23

[1]Data not included in calculations of gradients.

mer when the sockeye salmon migrate through these areas, the vertical and horizontal gradients are presumably smaller.

Available information indicates that salmon in general and sockeye in particular do not restrict themselves to one depth but rather have a diel vertical movement pattern while at sea. Manzer (1964) reported that most sockeye were caught in gill nets at or near the surface during the night, but in the daytime they were caught in substantial numbers as deep as 48 to 60 m. Mishima and Shimazaki (1969) reported a more complex pattern: sockeye were most abundant on the surface at 13:00-15:00 h but a second peak of abundance occurred at 03:00-05:00 h. Whereas variations in diel movements and depth distribution may occur, it seems likely that sockeye experience temperature changes of 1°C during their daily movements, and may experience changes of 4° to 5°C if they dive below the mixed layer.

The slight changes in temperature associated with horizontal movement relative to vertical movement make it unlikely that the long-distance migration of homing sockeye is determined by physiological responses to temperature (Laevastu 1983). Moreover, the temperatures experienced by sockeye salmon at sea do not seem to reflect physiological optima (Brett 1974, 1983). Nevertheless, there is a west-east gradient of increasing temperature over much of the homeward path of Fraser River sockeye salmon. Therefore, "predictive behavioural thermoregulation" (Neill 1979) may play a role in homing, though "reactive behavioural thermoregulation" (e.g., Olla et al. 1975) probably does not. However, gradients are an inefficient aid to migration unless

coupled with an independent sense of direction. Moreover, as the salmon near the coast, they may experience a decrease in temperature (Table 3).

We conclude that the relationship between sea surface temperatures at Kains Island and the diversion rate of sockeye salmon returning to the Fraser River via Johnstone Strait between 1978 and 1985 reflects the influence of ocean conditions on the behavior of fish, either on the feeding distribution prior to homing (see also Mysak 1986) or on the homing migration itself.

Fraser River Discharge and Sockeye Salmon Migration

Most of the fresh water along the British Columbia coast originates from the Columbia, Fraser, and Skeena Rivers and distinct tongues of dilute water (SSS of 32.6‰ and less) extend seaward from the Strait of Juan de Fuca and Queen Charlotte Sound several hundred kilometers offshore (Favorite 1961). Wickett (1977) suggested that it was the Fraser River water discharged in the ocean to the northwest of Vancouver Island that increased the percentage of Fraser River sockeye migrating through Johnstone Strait.

Fraser River sockeye migrating from their ocean feeding grounds towards the British Columbia coast pass through the areas of dilute surface water ("dilute domain") long before making landfall (Fig. 9). Interannual changes in river discharge and the resulting dilute extensions offshore could affect the coastal approach routes of Fraser River sockeye by causing more northerly landfall than usual during years of high levels of runoff (Favorite 1961; Wickett 1977).

What might be the mechanism that underlies a direct relationship between river discharge and migration route of adult Fraser River sockeye salmon? Two possibilities present themselves. First, returning sockeye salmon could prefer lower salinity water as they home, similar but

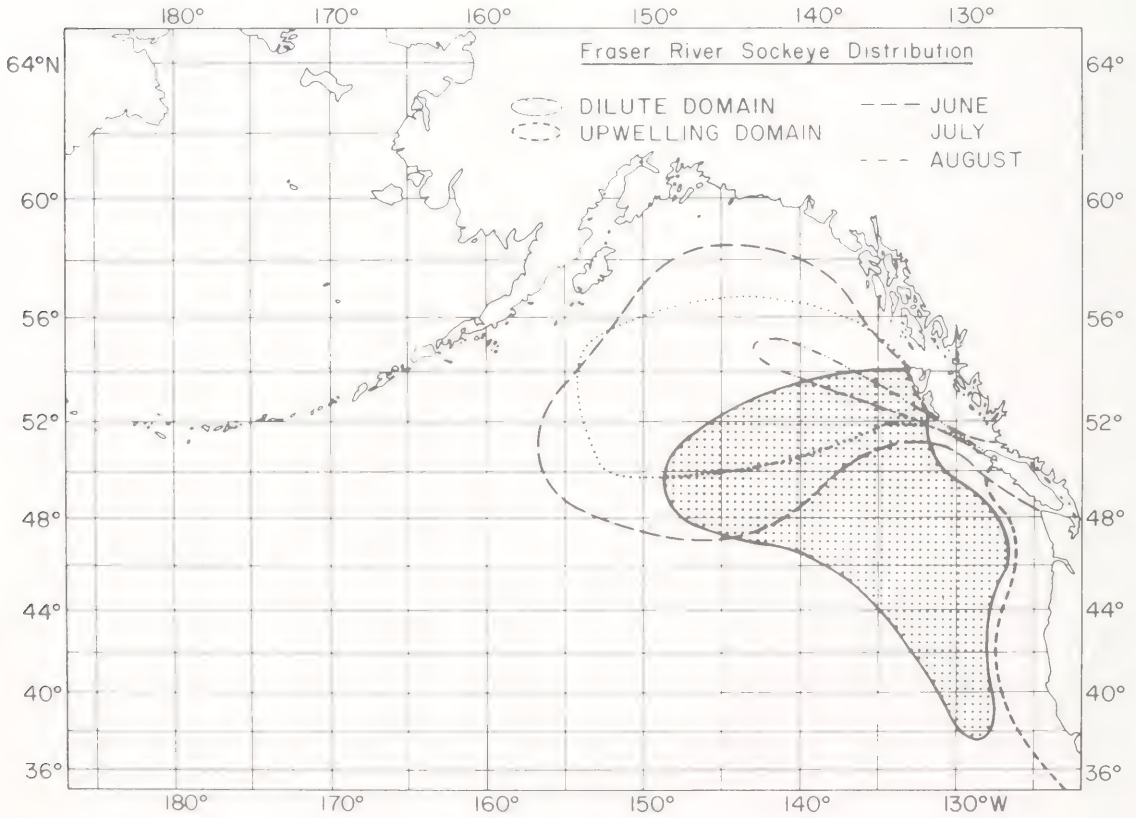


FIGURE 9.—The estimated distribution of maturing Fraser River sockeye salmon in June, July, and August in relation to regions of dilute water and upwelling.

opposite to the increasing saltwater preference documented by Baggerman (1960) and McInerney (1964) for juvenile salmon during the period of seaward migration. McInerney (1964) argued that the shift in salinity preference over time could gradually lead fish along the gradient of salinities found in coastal areas toward the open ocean.

Salinity measurements during the 1959 cruise (S.I.O.U.C 1965) mentioned previously showed that from the middle of the Gulf of Alaska to the tip of Vancouver Island, sea surface salinities decreased from 32.73 to 32.46‰ over a distance of about 1,757 km (Table 4). Fish swimming at a rate of 48 km/day would have met changes averaging 0.00015‰/km or 0.0074‰/day when approaching the coast. The threshold for recognition of salinity differences by sockeye salmon is unknown. However, if it is similar to that of minnows (*Phoxinus phoxinus*) of 0.003‰ (Glaser 1966), then it is about 20 times higher than the average difference that wil be encountered during a km of travel.

TABLE 4.—Salinity at depth, recorded by the RV *Brown Bear*, 16-24 July 1959 (data from S.I.O.U.C. 1965)

Latitude (N)	Longitude (W)	0 m	30 m	50 m
53°56′	153°18′	32.73	32.84	32.88
52°42′	149°43′	32.75	32.84	32.88
53°30′	146°42′	32.85	32.86	32.95
52°58′	143°27′	32.60	32.61	32.72
52°18′	139°35′	32.66	32.68	32.83
51°40′	135°55′	32.24	32.31	32.53
50°40′	131°57′	32.15	32.31	32.57
49°30′	128°12′	32.46	32.47	32.53
48°44′	125°39′	[1]31.35	[1]32.28	[1]32.73

[1]Data not included in calculations of gradients.

Moreover, salinity changes towards the coast do not occur in a smooth gradient (Table 4). Water masses of different salinities and temperatures form a dynamic patchwork that is continuously changing under the influence of wind and currents (Tabata 1984). We therefore consider it unlikely that a general preference for lower salinity water determines the approach direction of homing Fraser River sockeye migration. Smith (1985) concluded that for fishes in general ". . .there is little evidence that salinity is a guiding mechanism."

Second, the sockeye could react to home odors from the Fraser River in the offshore waters as suggested by Favorite (1961) and Wickett (1977). The sensitivity of salmonids to certain odors is high: 10^{-8} M for morpholine and 10^{-9} M for free amino acids (Brett and Groot 1963; Hara et al. 1984). However, it is questionable that, given the extensive mixing in the Fraser River and in the ocean, the already low concentrations of odors from the different nursery lakes would be above threshold. Moreover, odors generally act as releasers and not as directors of responses (Johnsen and Hasler 1980). It is difficult to understand how salmon could change their migration routes far offshore in the ocean, even if they could sense the aroma of their home water. We therefore conclude that the relationship between Fraser River discharge and diversion rate of sockeye salmon returning via the northern route is not a direct, but probably an indirect one.

CONCLUSION

We hypothesize that Fraser River discharge (1953-77) and SST at Kains Island (1978-85) primarily reflect certain atmospheric and related oceanographic conditions, which affect Fraser River sockeye salmon winter distribution and/or migration in the ocean. The weather conditions in the Gulf of Alaska are controlled by the locations and intensities of two major semipermanent atmospheric pressure cells; the Aleutian low and the North Pacific high (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985). The interannual variations of these pressure cells affect precipitation and the extent of the snow pack during the winter, as well as temperature, salinity, and circulation patterns in the ocean (Favorite et al. 1976; Thomson 1981; Emery and Hamilton 1985).

Anomalous temperature conditions in the ocean, resulting from varying atmospheric conditions, may affect salmon migrations directly or indirectly by acting on their feeding distribution or on the distance or direction they must travel to reach home. When ocean conditions are warmer than usual, sockeye salmon tend to encounter the coast of British Columbia at the north of Vancouver Island. In such cases their approach to the Fraser River will be primarily through Johnstone Strait. Following cold winter conditions in the Gulf of Alaska, landfall usually occurs along the west coast of Vancouver Island and migration to the home river is primarily via the Strait of Juan de Fuca.

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PREDATION ON *CAPITELLA* SPP. BY SMALL-MOUTHED PLEURONECTIDS IN PUGET SOUND, WASHINGTON[1]

D. SCOTT BECKER[2] AND KENNETH K. CHEW[3]

ABSTRACT

This study examined the predation patterns of three flatfishes (English sole, Dover sole, and rex sole) on the opportunistic polychaetes *Capitella* spp. in disturbed soft-bottom habitats of Puget Sound, Washington. Sampling was conducted throughout the diel cycle during May and June 1981. All three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Numerical dietary contribution by *Capitella* spp. was greatest at night for all three fishes, suggesting that these polychaetes become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter their normal diurnal feeding chronology and forage successfully at night. This study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

The composition of soft-bottom marine benthic invertebrate assemblages can be altered by a variety of natural and anthropogenic disturbances, including salinity reduction (Boesch et al. 1981), storm-induced surge (Rees et al. 1977), hypoxia (Santos and Simon 1980), dredge-spoil dumping (Rhoads et al. 1978), sewage disposal (Pearson and Rosenberg 1978), and oil spills (Sanders et al. 1980). To predict the effects of these events on demersal fishes, predator-prey relationships between benthic invertebrates and their piscine predators must be understood. Unfortunately, this kind of information is rare for marine ecosystems (Mills 1975).

Frequently, benthic invertebrate assemblages in disturbed habitats are dominated by one or more opportunistic species (e.g., Grassle and Grassle 1974; McCall 1977; Pearson and Rosenberg 1978; Rhoads et al. 1978). These opportunists are adapted to rapidly colonize disturbed environments and often attain exceptionally high population densities. Because many of these species reside at or near the sediment-water interface, they represent a potential food bonanza to bottom-feeding demersal fishes. When fishes encounter such an abundant and accessible food source, it seems likely that those species capable of modifying their foraging behavior to fully exploit this windfall will do so. Such opportunistic predation on temporally or spatially variable superabundant prey has been found for a variety of fishes (e.g., Nilsson 1960; Ivlev 1961; Zaret and Rand 1971; Murdoch et al. 1975), and is one prediction of optimal foraging theory (review in Pyke et al. 1977).

As an example of how a group of demersal fishes responds to a disturbed soft-bottom habitat dominated by opportunistic benthic invertebrates, we describe the foraging patterns of three flatfishes (Pleuronectidae) in Puget Sound, WA on *Capitella* spp., a well-known group of opportunistic polychaetes (Grassle and Grassle 1974; Pearson and Rosenberg 1978). The flatfishes targeted for study were English sole, *Parophrys vetulus*; Dover sole, *Microstomus pacificus*; and rex sole, *Glyptocephalus zachirus*. These fishes belong to the small-mouthed subgroup of pleuronectids identified by Moiseev (1953) and, as such, prey primarily upon small infaunal and epifaunal benthic invertebrates. These species also form a major component of demersal fish assemblages in Puget Sound (Miller et al. 1977; Wingert and Miller 1979; Becker 1984), as well as in most nearshore areas along the west coasts of the United States and Canada (e.g., Alverson et al. 1964; Day and Pearcy 1968; Hart 1973; Allen 1982).

MATERIALS AND METHODS

Field Sampling

The study was conducted on the delta of the

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Puyallup River, in Puget Sound's Commencement Bay (Fig. 1). This dynamic area receives a variety of anthropogenic and natural discharges. For example, the river discharges approximately 5,500 kg/year of sediments in a seasonally variable manner (Dexter et al. 1981). In addition, the City of Tacoma releases primary-treated sewage into the river at an annual flow rate of 0.9 m^3/second (20.5 MGD) approximately 2.4 km upstream from the river mouth (Tetra Tech 1981). A preliminary survey conducted by the authors showed that benthic invertebrate assemblages throughout much of the delta were dominated numerically by *Capitella* spp.

Field sampling was conducted from 26 May to 3 June 1981. All three target species have spawned by this time (Hart 1973) and, as typical of most adult pleuronectids, are presumably feeding intensely to replenish the energy used previously for migration, overwintering, and spawning (e.g., Moiseev 1953; Roff 1982).

Sampling was conducted along two 300 m transects located at a depth of 32 ± 2 m (Fig. 1). This depth corresponds to the upper boundary of the

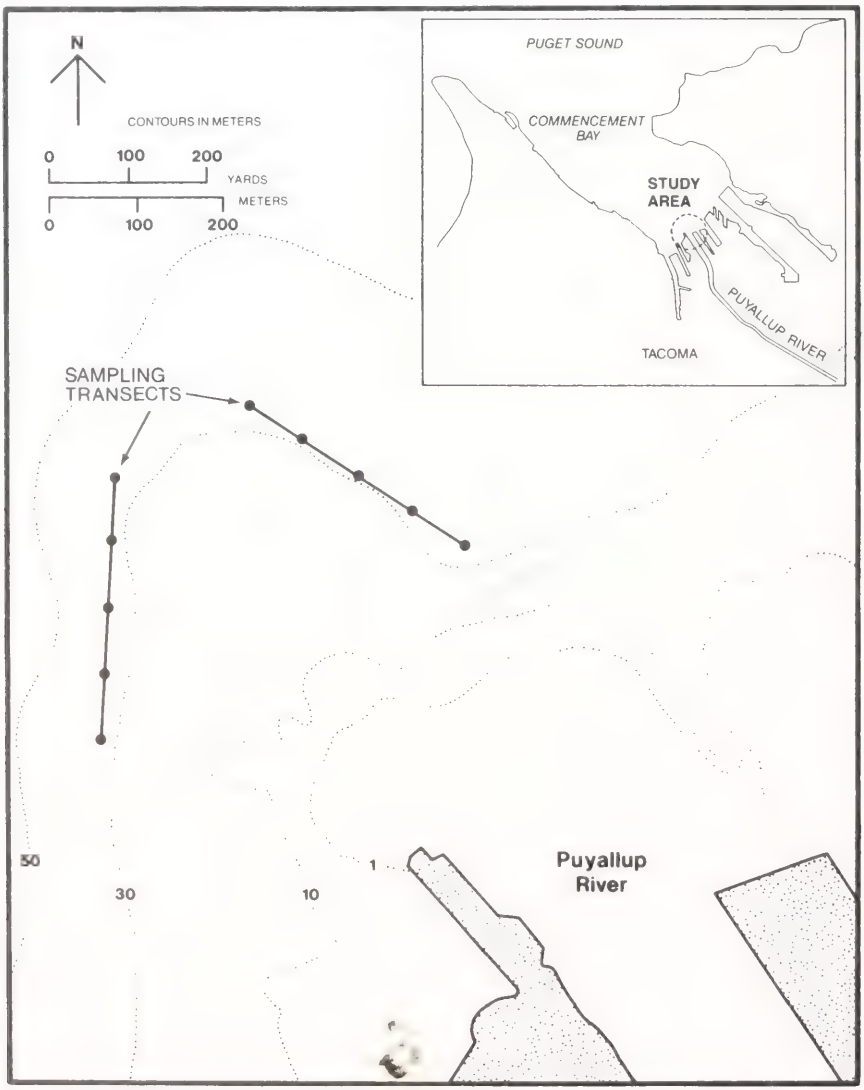

FIGURE 1.—Locations of sampling transects and benthic sampling points (i.e., large dots) along each transect.

intermediate faunal zone (i.e., 30-70 m depth) identified for Puget Sound demersal fish assemblages by Wingert and Miller (1979). All three target species are sufficiently abundant in this depth zone to allow a quantitative food habits analysis to be conducted. Data from both transects were pooled prior to analysis.

Fishes were collected using a 7.6 m (headrope) otter trawl having a body mesh size of 3.2 cm (stretched) and a cod-end liner mesh size of 0.8 cm (stretched). Trawling was conducted along both transects at a constant vessel speed of approximately 2.5 kn. All positioning was achieved using the LORAN-C navigation system. To assess diel variations in feeding behavior, hauls were made along each transect during four periods of the diel cycle: morning (0900-1030 h), afternoon (1300-1500 h), evening (1900-2030 h), and night (2330-0100 h). Each transect was sampled twice during each time period, yielding eight hauls per transect or a total of 16 hauls for the study.

At sea, the stomach contents of the target species were fixed by injecting, using a 50 cc syringe, a 10% solution of buffered formalin into the body cavity of each individual. These fishes were then brought to the laboratory and stored at 4°C.

Benthic invertebrates along each transect were sampled within 2 days of trawling. Organisms were collected using a 0.1 m^2 van Veen bottom grab, sieved through a 1.0 mm mesh screen, fixed with a 10% solution of buffered formalin, and transferred to 70% ethanol for storage. A single grab sample was taken during daytime at each of five sampling points positioned at approximately equal distances along each transect (Fig. 1).

Laboratory Analysis

Within 5 days of sampling, the total length (TL) of each fish was measured to the nearest 1.0 mm. The body cavity was then opened and the stomach was removed by severing the esophagus and pylorus. Stomachs were stored in 70% ethanol prior to analysis.

For food habits analysis, stomachs were subsampled from the total pool of available stomachs. To minimize within-species variation as a result of size-dependent foraging patterns (e.g., Gabriel and Pearcy 1981), only individuals within an 80 mm length range were selected for analysis. The ranges used for English sole, Dover sole, and rex sole were 240-320, 200-280, and 210-290 mm TL, respectively. Each length range bracketed the median length observed for each species.

Identifications of all invertebrates in stomachs and benthic samples were made using a dissecting microscope. Sizes of all *Capitella* spp. were estimated using the width of the fifth setiger (cf. Tsutsumi and Kikuchi 1984). This measurement was used instead of body length because many of these polychaetes were fragmented during grab sampling or ingestion by the fishes. Setiger widths were measured to the nearest 0.1 mm using an ocular micrometer.

The dietary contribution of *Capitella* spp. to the total stomach contents of each target species was estimated using percentages based on numerical proportions. In addition, the total number of prey per stomach (i.e., *Capitella* spp. plus all other organisms) was used as an index of feeding intensity for each species.

Statistical Analysis

Nonrandom predation on *Capitella* spp. (i.e., selection) was tested by comparing the numerical proportions of these polychaetes in the stomachs of the fishes with the proportion found in the benthos using a 2×2 contingency formulation and the chi-square criterion (Pearre 1982). Direction of selection was determined by inspecting the relative proportions of prey in the stomachs and benthos. Nonrandom size selection of *Capitella* spp. was tested by comparing the size distributions of these polychaetes in the stomachs of the fishes with the size distribution found in the benthos using the Mann-Whitney U-test. In both of these analyses, four comparisons (i.e., one for each time period) for each species were made with a single set of benthic observations. Because these four comparisons lacked independence, significance levels were adjusted conservatively using Bonferroni's technique (Miller 1981).

To examine how the foraging patterns of English sole differed between habitats where benthic assemblages were dominated by *Capitella* spp. and habitats where assemblages did not include these polychaetes, the values of feeding intensity (i.e., numbers of prey per stomach) found in the present study were compared with those obtained at six other sites in Puget Sound by Becker (1984). These six sites were located at depths between 12 and 32 m, and fishes were sampled and processed using methods identical to those described for the present study. Values of feeding intensity were compared during each period of the diel cycle using the Mann-Whitney U-test. Similar analyses could not be conducted for Dover

sole and rex sole because these fishes were not sufficiently abundant at the six additional sites.

RESULTS

Prey Selection

Throughout the diel cycle, the numerical proportion of *Capitella* spp. in the diets of all three fishes exceeded the proportion of these polychaetes in the benthos (Table 1). Selection of *Capitella* spp. was highly significant ($P < 0.001$) during all four time periods for English sole and rex sole, and during morning and night for Dover sole. Selection was significant at $P < 0.01$ during evening for Dover sole, but not significant ($P > 0.05$) during afternoon for this species.

TABLE 1.—Comparisons of proportions of *Capitella* spp. in fish stomachs with the proportion in the benthos using a 2 × 2 contingency test. **P < 0.01, ***P < 0.001, ns = P > 0.05 (experimentwise).

	Number of *Capitella* spp./Total number of prey[1,2]			
Species	Morning	Afternoon	Evening	Night
English sole	508/1,464*** (50)	425/1,029*** (40)	1,072/1,596*** (32)	1,904/2,592*** (56)
Dover sole	329/861*** (35)	114/416 ns (21)	200/612** (36)	218/461*** (36)
Rex sole	456/526*** (16)	272/412*** (18)	209/276*** (15)	603/671*** (19)

[1]Number of stomachs examined is given in parentheses.
[2]Proportion of *Capitella* spp. in the benthos was 904/3,517.

Percent numerical contribution by *Capitella* spp. to the total diet varied considerably among the three fishes (Fig. 2). Rex sole showed the greatest preference for these polychaetes, including them in 66-90% of the diet throughout the diel cycle. By contrast, Dover sole exhibited the least preference for *Capitella* spp., including them in only 27-47% of the diet. English sole showed moderate preference for these polychaetes, including them in 35-73% of the diet. Diel variation of feeding intensity closely paralleled dietary contributions of *Capitella* spp. for English sole and rex sole, with both variables peaking at night (Fig. 2). For Dover sole, however, these two variables followed substantially different diel trends, with percent dietary contribution of *Capitella* spp. reaching its maximum and feeding intensity dropping to its minimum at night.

Although the magnitudes of percent dietary contribution by *Capitella* spp. differed among the three fishes, several similarities existed in the diel variation of these values (Fig. 2). Minimum dietary contributions were found during morning (English sole) or afternoon (Dover sole and rex sole), whereas maximum contributions were found at night (all three fishes).

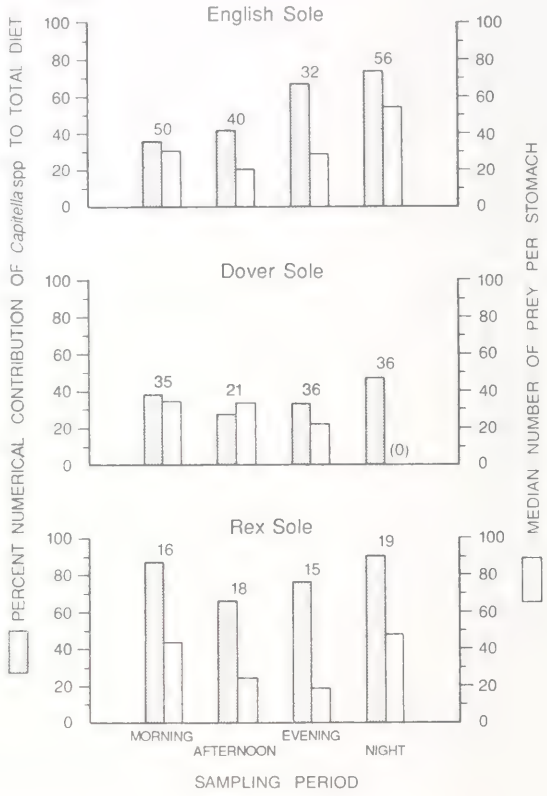

FIGURE 2.—Diel predation patterns of the target species. Number of stomachs examined is presented above each pair of bars.

Prey Size Selection

Median size of *Capitella* spp. in stomachs exceeded the median size of these polychaetes in the benthos during all four time periods for English sole and rex sole, and during morning, afternoon, and night for Dover sole (Fig. 3). Median prey size for Dover sole during evening was approximately equal to median size of *Capitella* spp. in the benthos. Size differences of *Capitella* spp. between diets and the benthos were highly significant ($P < 0.001$) during all four time periods for rex sole, during morning, afternoon, and night for English sole, and during morning and afternoon for Dover sole. Size differences were significant at

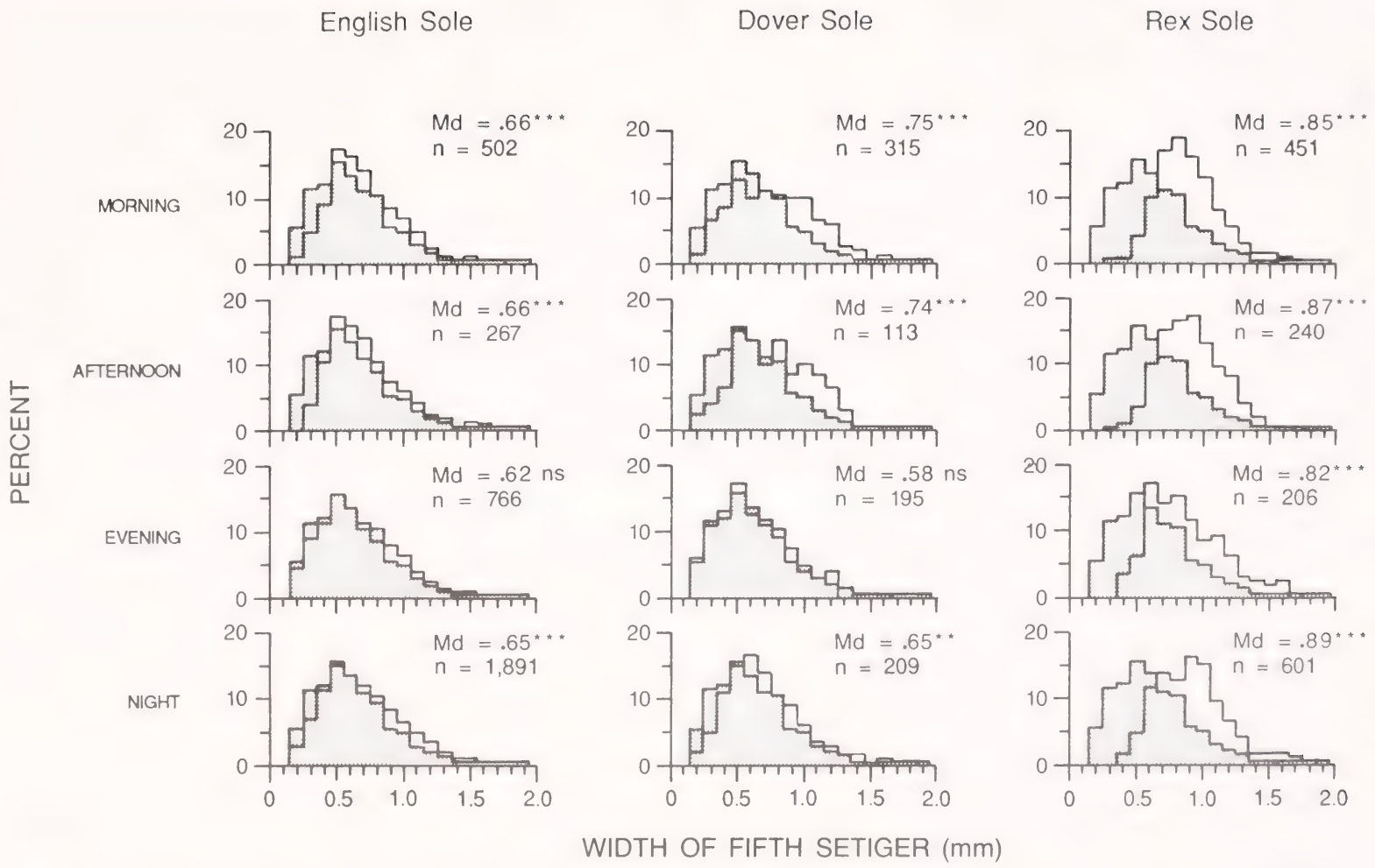

FIGURE 3.—Comparisons of size distributions of *Capitella* spp. in fish stomachs (i.e., open distributions) with the size distribution in the benthos (i.e., stippled distribution) using the Mann-Whitney U-test. Median size (Md) and sample size (n) are given with each distribution from the stomachs. Median size in the benthos was 0.59 mm and sample size was 898 individuals. $^{**}P < 0.01$, $^{***}P < 0.001$, ns = $P > 0.05$ (experimentwise).

$P < 0.01$ during night for Dover sole. No significant size differences ($P > 0.05$) were found during evening for English sole and Dover sole.

Of the three fishes, rex sole selected the largest *Capitella* spp. during every time period, with median size ranging from 0.82 to 0.89 mm throughout the diel cycle. Median size of *Capitella* spp. selected by English sole and Dover sole ranged from 0.62 to 0.66 mm and 0.58 to 0.75 mm, respectively.

Habitat Comparisons

Differences in number of prey per stomach between English sole captured in habitats where *Capitella* spp. were present and conspecifics captured in habitats where these polychaetes were absent were highly significant ($P < 0.001$) at night, but not significant ($P > 0.05$) during morning, afternoon, and evening (Fig. 4). The diel trends of feeding intensity in the two habitats were strikingly different. Where *Capitella* spp. were present, feeding intensity increased from afternoon to evening, and then peaked at night (median = 53.5 prey per stomach). By contrast, in habitats where *Capitella* spp. were absent, feeding intensity declined from afternoon to evening, and reached a minimum (median = 0 prey per stomach) at night.

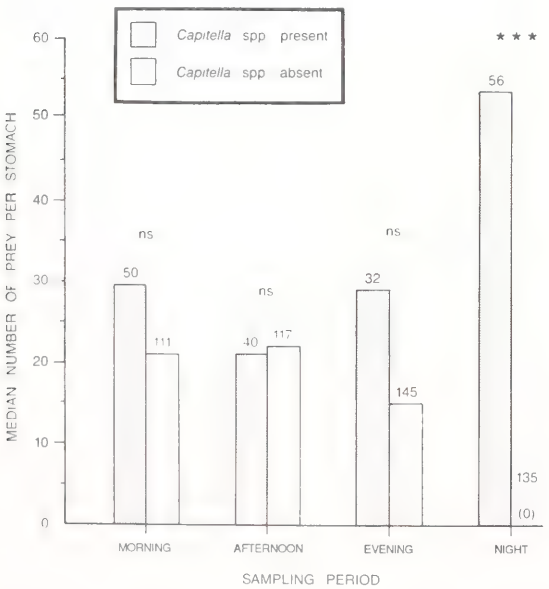

FIGURE 4.—Comparisons of values of feeding intensity for English sole between habitats with and without *Capitella* spp. using the Mann-Whitney U-test. Number of stomachs examined is presented above each bar. Significance level is given above each pair of bars. ***P < 0.001, ns = P > 0.05.

DISCUSSION

Although *Capitella* spp. accounted for only 25.7% of benthic individuals, their importance as prey to English sole, Dover sole, and rex sole was substantial. All three fishes exhibited significant ($P < 0.05$) numerical and size selection of these polychaetes during all or most of the diel cycle. Based on literature accounts of the food habits of these fishes, the observed importance of *Capitella* spp. as prey could not have been predicted directly.

Most historical accounts of the food habits of the three fishes do not identify *Capitella* spp. as prey (e.g., Hagerman 1952; Kravitz et al. 1977; Hulberg and Oliver 1978; Pearcy and Hancock 1978; Gabriel and Pearcy 1981; Allen 1982; Hogue and Carey 1982). However, most of these studies were conducted in areas where *Capitella* spp. generally would not be expected to occur in large numbers in the benthos (i.e., the continental shelf off Oregon and California). At least two studies have found that one or more of these fishes consume *Capitella* spp. Cross et al. (1984) examined the food habits of English sole ($n = 13$) and Dover sole ($n = 38$) in areas influenced by sewage discharges off Los Angeles, CA. Although *C. capitata* numerically accounted for 40-95% of benthic assemblages, the dietary contributions by this polychaete were small (i.e., 0% for English sole and <10% for Dover sole). Toole (1980) found that *C. capitata* was a major prey item of juvenile English sole (66-102 mm TL, $n = 45$) captured on an intertidal sand flat in Humbolt Bay, CA. However, because benthic assemblages were not sampled, it is unknown whether these fish were preying nonrandomly on *C. capitata*.

Of the three fishes sampled in the present study, rex sole exhibited the greatest degree of selective predation on *Capitella* spp. This species was the only one to nonrandomly select *Capitella* spp. based on both prey number and prey size throughout the diel cycle. In addition, rex sole selected the largest *Capitella* spp. of the three fishes, and included these polychaetes in the largest percentage of total diet during all four time periods. The observed peak in feeding intensity at night agrees with past descriptions of rex sole as a nocturnal forager (Kravitz et al. 1977; Allen 1982; Becker 1984). The concomitant peak in percent dietary contribution of *Capitella* spp. at

night indicates that when rex sole were feeding most intensely, selection of *Capitella* spp. was at its highest level.

Dover sole was the least selective of the three fishes with respect to predation on *Capitella* spp. This species did not exhibit selective predation based on prey number during afternoon, nor based on prey size during evening. In addition, the percent dietary contribution by *Capitella* spp. for Dover sole was the smallest of the three fishes during three of the four time periods. The observed minimum level of feeding intensity at night is consistent with the description of Dover sole as a diurnal forager (Allen 1982; Becker 1984). The nighttime peak in percent dietary contribution by *Capitella* spp. suggests that even though this fish normally does not forage at night, *Capitella* spp. could be captured quite successfully relative to other benthic invertebrates.

English sole was intermediate between rex sole and Dover sole with respect to degree of selective predation on *Capitella* spp. Although this species selectively consumed these polychaetes based on prey number throughout the diel cycle, prey size selection was not observed during evening. In addition, dietary contribution by *Capitella* spp. for English sole was the smallest of the three fishes during morning, but intermediate in magnitude during the remainder of the diel cycle. The observed peak in feeding intensity at night is contradictory to the description of English sole as a diurnal forager (Allen 1982; Hogue and Carey 1982; Becker 1984). Because dietary contribution of *Capitella* spp. peaked at a high level of 73% at night, much of the ability of English sole to forage at night resulted from predation on these polychaetes. The influence of *Capitella* spp. on nocturnal foraging by English sole was confirmed by the comparison of diel variation of feeding intensity in habitats with and without *Capitella* spp.

The observed diel variations of predation on *Capitella* spp. could have resulted from behavioral differences of either the fishes or the polychaetes. Because the fishes were sampled throughout the diel cycle, much of the variation due to the predators was accounted for. However, because diel variation in behavior of *Capitella* spp. could not be evaluated using the sampling methods employed in this study, variation in prey availability is unknown. However, at least one pattern is suggested. Because dietary contribution by *Capitella* spp. peaked at night for all three fishes, these polychaetes may become more active at the sediment surface and thus more vulnerable to predation at night. The ability of English sole to alter its normal diurnal feeding chronology to forage primarily on *Capitella* spp. at night further suggests that these polychaetes become more accessible at night. Levinton (1971) found that the bivalve *Macoma tenta* foraged primarily at night and suggested that this periodicity was used, in part, to avoid diurnal predators (primarily winter flounder, *Pseudopleuronectes americanus*). Although this defense mechanism may succeed with obligate diurnal predators, it would not be effective in avoiding nocturnal predators (e.g., rex sole) or species capable of modifying their normal diurnal feeding chronology (e.g., English sole).

From an applied standpoint, results of this study have several implications regarding the concept of disturbance management described by Rhoads et al. (1978). Those authors suggested that by properly managing habitat disturbance (i.e., dredge-spoil disposal in their case), benthic invertebrate assemblages can be maintained in the early successional stages when they are dominated by pioneering species, including opportunists such as *Capitella* spp. Because productivity of these early successional stages generally exceeds that of later stages, Rhoads et al. (1978) hypothesized that benthic assemblages dominated by pioneering species represent an enhanced food resource for demersal fishes. The observed importance of *Capitella* spp. as prey for the three fishes considered in the present study supports this hypothesis. For example, all three fishes selectively preyed upon *Capitella* spp. throughout all or most of the diel cycle, and English sole was able to modify its normal diurnal feeding chronology to prey primarily on these polychaetes at night.

Although the hypothesis of Rhoads et al. (1978) is supported by the present study, enhancing the productivity of a food resource may not be beneficial to demersal fishes if the nutritional quality of their diet is reduced in the process. For example, a variety of fish diseases have been attributed, in part, to dietary deficiencies or imbalances of specific nutrients (reviews in National Research Council 1977, 1981). In addition, the toxicity of chemical contaminants to fishes may be enhanced as a result of improper diets (e.g., Mehrle et al. 1977). Although *Capitella* spp. accounted for only 25.7% of the benthic invertebrates sampled in the present study, the dietary contributions of these polychaetes generally were much greater, especially for rex sole. Given the influence of a balanced diet on fish health, it is possible that pro-

longed dietary restriction to one or several opportunistic prey could compromise the health of the fishes.

In summary, all three fishes exhibited some degree of selective predation on *Capitella* spp. based on both number and size of these prey. Dietary contribution by these polychaetes was greatest at night for all three fishes, suggesting that *Capitella* spp. may become more accessible to predators at night. Predation on *Capitella* spp. allowed English sole to alter its normal diurnal feeding behavior and forage successfully at night. Finally, this study supports the hypothesis that some demersal fishes can exploit opportunistic prey in disturbed habitats.

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THE REPRODUCTIVE BIOLOGY OF WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, IN THE BERING SEA, WITH REFERENCE TO SPAWNING STOCK STRUCTURE

SARAH HINCKLEY[1]

ABSTRACT

The reproductive biology of walleye pollock, *Theragra chalcogramma*, in the Bering Sea was studied from collections of ovaries and observations of spawning in 1984. Spawning occurred in the Aleutian Basin from January through March, in the southeastern Bering Sea from March through June, and northwest of the Pribilof Islands from June through August. Spawning concentrations found in these areas showed significant differences in length at age and fecundity. Histological evidence indicated that the spawning period of an individual female probably lasts less than 1 month. Results indicate at least three separate spawning stocks of walleye pollock within the Bering Sea. These are located in the Aleutian Basin, over the southeastern continental shelf and slope and northwest shelf areas, and over the continental slope northwest of the Pribilof Islands. Mixing of stocks between widely separated spawning grounds due to extended spawning and migration is not likely.

Walleye pollock, *Theragra chalcogramma*, a member of the gadid family found in the North Pacific Ocean, currently supports the largest single-species fishery in the world. In the eastern portion of its range, catches of pollock average 100,000 to 300,000 metric tons (t) per year in the Gulf of Alaska (Alton et al. in press) and 1,000,000 t per year in the Bering Sea (Bakkala et al. in press). The walleye pollock resource in the Bering Sea is presently managed as a single stock but there is increasing evidence that substocks may exist (Lynde et al. 1986[2]). If substocks exist, this information should be considered in management strategy.

If a stock is defined as a production unit or a group of fish showing similar responses to environmental conditions within a certain geographic area, then population characteristics such as growth rates, fecundity, and size or age at maturity may provide the most practical means of differentiating these units. As these parameters determine the yield of a stock to a fishery, identification of production units based on some or all of them may improve the effectiveness of fisheries management.

A clearer understanding of the reproductive process in walleye pollock may also aid in differentiating stocks or production units. Nishiyama and Haryu (1981) proposed that walleye pollock in the Bering Sea may migrate and spawn over extensive distances during the long spawning season, implying that spawning groups mix over large areas. Sakurai (1982) has shown in laboratory experiments that walleye pollock spawn a single group of matured eggs in successive batches, possibly over a period of 1 month. It is not known, however, whether an individual female is capable of repeating vitellogenesis with more than one separate group of eggs in 1 year (i.e., of rematuring the ovary). Evidence of batch spawning or rematuration in Bering Sea walleye pollock may indicate the duration of individual spawning and the potential for mixing between spawning concentrations found in widely separated areas.

In this study, the spatial and temporal distribution of spawning for 1984 has been documented and the length at age and fecundity of walleye pollock from spawning concentrations in different areas has been determined. Walleye pollock ovaries were examined histologically to clarify the process of oocyte development, to learn whether annual fecundity is determinate or indeterminate and to learn the optimal stage for estimating fecundity, and to determine whether

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[2]Lynde, C. M., M. Van Houghton Lynde, and R. C. Francis. 1986. Regional and temporal differences in growth of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea and Aleutian Basin with implications for management. NWAFC Proc. Rep. 86-10. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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batch spawning or rematuration occur in Bering Sea pollock.

METHODS

Data and Sample Collection

Data and specimens of walleye pollock were collected from December 1983 to October 1984 by National Marine Fisheries Service (NMFS) observers aboard foreign commercial fishing vessels and by NMFS pesonnel aboard NOAA research vessels. Data collection was divided into three phases. First, fisheries observers logged the time and location of commerical hauls in which spawning walleye pollock (those with running eggs or milt) were observed. A total of 1,538 observations was made between January and October. Second, otoliths were collected from walleye pollock in hauls where spawning was observed. Third, walleye pollock ovaries were collected for histology and anaylsis of fecundity. Three ovaries per maturity stage (Hinckley 1986) were collected and preserved in 10% neutral buffered formalin for histological analysis. A separate collection of late developing or mature ovaries was made for the fecundity analysis. Five ovaries per 5 cm length interval were collected over the entire length range encountered. These ovaries were preserved in modified Gilson's solution (Ito 1977[3]). A total of 345 ovaries were collected for histology and 294 for fecundity analysis.

Data and Sample Processing

Location of Spawning and Length at Age of Spawners

Spawning locations of walleye pollock were plotted by month. The distribution of fishing effort by the foreign commercial fleet over the spawning season was examined and compared with locations where spawning was found. Water temperatures and depths of capture at spawning locations were also examined.

For the length-at-age analysis, five areas were defined within the Bering Sea based on oceanographic features (after Lynde et al. fn. 2): the southeast continental shelf, the southeast continental slope, the northwest shelf, the northwest slope, and the Aleutian Basin (Fig. 1). Northwest and southeast areas were divided at the Pribilof Islands and buffer zones were defined in order to clearly separate them. Ages were assigned to a maximum of 200 otoliths per area by readers at the Northwest and Alaska Fisheries Center (NWAFC) age and growth laboratory.

Lynde et al. (fn. 2) found that walleye pollock from the Aleutian Basin and the northwest slope were generally slower growing than pollock from the southeast shelf and slope areas. Based on this observation, R. Francis and A. Hollowed[4] classified walleye pollock as "northern" (slow-growing) or "southern" (fast-growing), and developed two corresponding growth curves. In the present study, the growth of walleye pollock from spawning concentrations in different areas was compared to the two growth curves described in Francis and Hollowed's unpublished study. The geographical distribution of the two growth types was then examined.

To derive their "northern" and "southern" growth curves, Francis and Hollowed (unpubl. data) used age data collected by foreign fisheries observers from 1978 to 1983. Age samples were separated into $\frac{1}{2}°$ latitude by 1° longitude cells. The mean length at age was estimated for each cell by year, quarter, and sex.

Estimates of mean length at age for each cell were used to classify the cell as "northern", "southern", or "unknown". The "northern" classification indicated that the distribution of mean length at age in a given cell was similar to that seen by Lynde et al. (fn. 2) in the northwest slope and Aleutian Basin areas (Fig. 1). The "southern" classification indicated that growth was similar to that observed by Lynde et al. (fn. 2) in the southeast slope and shelf areas (Fig. 1).

For this classification, the von Bertalanffy (1938) growth model was fitted to the weighted mean length-at-age data for the "northern" and "southern" areas for each quarter and sex over a period of 6 years (1978-83) (Lynde et al., fn. 2). The model was fitted using the BMDP PAR derivative-free nonlinear least squares estimation procedure (Dixon 1983) to produce predicted mean lengths at age for "northern" and "southern" fish.

[3]Ito, D. H. 1977. Fecundity of the copper rockfish, *Sebastes caurinus* (Richardson), from Puget Sound, Washington. Unpubl. manuscr. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

[4]Robert Francis and Anne Hollowed, Northwest and Alaska Fisheries Center, National Marine Fisheries Service NOAA, 7600 Sand Point Way N.E, Seattle, WA 98115, pers. commun. January 1985.

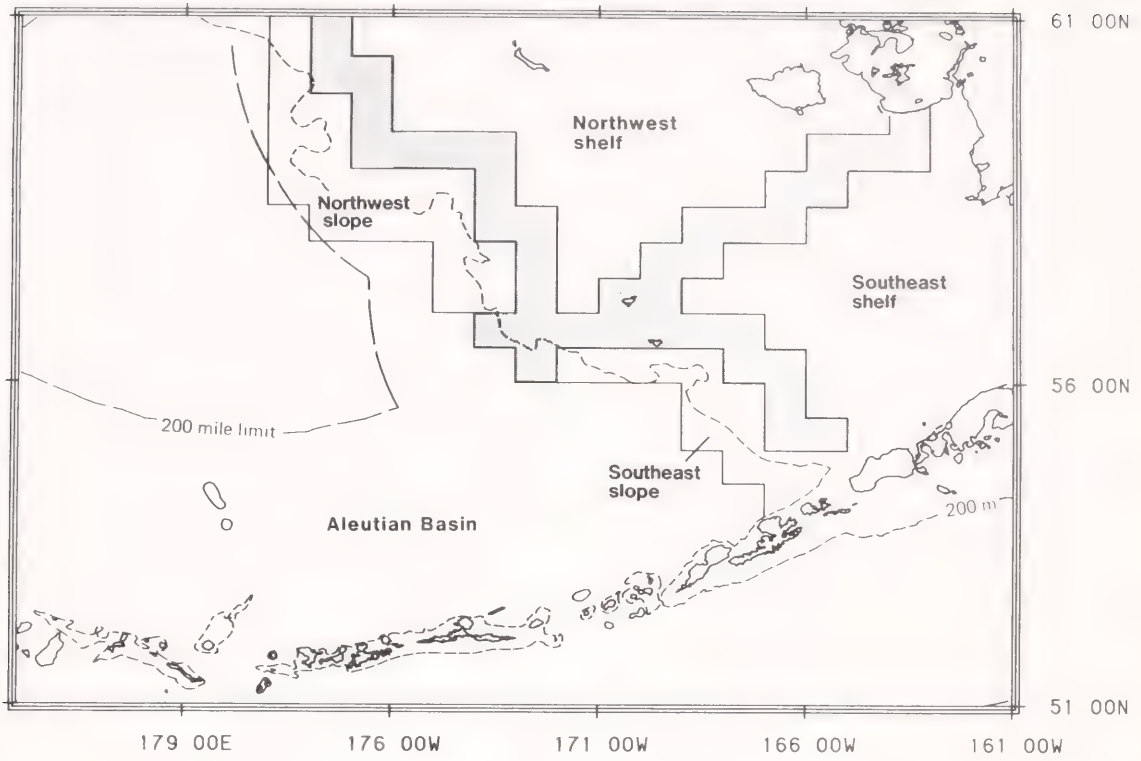


FIGURE 1.—Sampling areas within the Bering Sea. Shaded areas are buffer zones.

The cells were then classified for each sex and quarter using an index of similarity, $Pr(s)$. This index was based on the ratio of the sum of squared deviations of the observed mean length at age from the 6-yr fitted average for the southern region, to the sum of the squared deviations of the observed mean length at age from the southern and northern regions combined:

$$Pr(s) = 1 - [SS(s)/SS(s) + SS(n)]$$

where $SS(s) = \sum_{i=1}^{k} [X(i) - ES(i)]^2$ and

$$SS(n) = \sum_{i=1}^{k} [X(i) - EN(i)]^2.$$

$SS(s)$ = the sum of squared deviations for the southern regions,
$SS(n)$ = the sum of squared deviations for the northern regions,
$ES(i)$ = the 6-yr fitted average from the southern region,
$En(i)$ = the 6-yr fitted average from the northern region,
i = age,
$X(i)$ = the observed mean length at age (i),
k = the maximum age observed.

Thus, $Pr(s)$ is the likelihood of the cell being a southern cell. Arbitrary cut-off values of 0.75 and 0.25 were imposed to classify the southern and northern cells, respectively. Any value >0.25 and <0.75 defined an unknown cell.

New 6-yr average growth curves were fitted for each region by quarter and sex using only those estimates of mean length at age from cells that were classified as northern or southern (i.e., excluding all unknown cells). Partial F-tests showed ($P < 0.001$) that there are significant regional differences in growth between the "southern" (southeast shelf and slope) and the "northern" (Aleutian Basin and northwest slope) areas.

Using the new 6-yr average growth curves, the 1984 data were divided into cells, compared to Francis and Hollowed's (unpubl. data) growth curve, and were classified as northern, southern, or unknown, based on the index of similarity [$Pr(s)$] for both sexes combined:

$$Pr(s) = 1 - [SS(s)_{♀} + SS(s)_{♂}/SS(s)_{♀} + SS(s)_{♂} + SS(n)_{♀} + SS(n)_{♂}]$$

The classification of the 1984 data was examined to see whether the northern and southern cells fell into the same geographic areas as those which originally defined the growth types described by Lynde et al. (fn. 2) and the growth curves of Francis and Hollowed (i.e., the northwest slope and Aleutian Basin areas or the southeast shelf and slope areas).

Analysis of Fecundity

Collections of walleye pollock ovaries for fecundity analysis were subsampled by geographic area to provide at least four ovaries in each 5 cm length interval over the entire available length range. Ovaries were collected from walleye pollock in all areas except the northwest shelf, where observer coverage was inadequate. The oocytes were separated from the ovarian tissue by washing them through successively finer meshed sieves; and a volumetric subsampling method, similar to that described in Gunderson (1977), was used to estimate the total number of oocytes in each ovary. In all ovaries examined, there was a clear separation in the sizes of unyolked (uncounted) and yolked (counted) oocytes. The histological analysis (described below) indicated that ovaries showing this separation in egg size modes were at the stage of maturity suitable for fecundity counts. A minimum of five subsamples were counted for each ovary; if the coefficient of variation between subsample counts exceeded 10%, more counts were done, to a maximum of 10 counts. It was discovered that recounts of individual subsamples accounted for very little of the overall variation between counts, so these were not done on a regular basis.

The average coefficient of variation between subsample counts for each ovary was 5.20% (range, 0.87 to 10.30%). The number of oocytes was estimated for a total of 115 ovaries.

Fork length, ovary-free weight, and the mean of the subsample estimates of fecundity for each fish were used to derive three relationships for each area within the Bering Sea: length-fecundity, length-weight, and weight-fecundity. Nonlinear least-squares regression methods (Dixon 1983) were used to estimate parameters for each relationship. Unequal error variances were observed in the dependent variables of weight and fecundity. This was accounted for by the use of weighting factors in the nonlinear regression procedure. The weighting factor used was the inverse of the variance of the dependent variable.

Because comparison of linear regressions is the most direct method and because the linear and nonlinear regressions showed the same relative positions for each area, Newman-Keuls multiple range tests (Zar 1974) were done on the slopes and intercepts of the equations resulting from the linear regressions, to examine differences in the relationships by area. The regressions were fitted to a length range (38 to 60 cm) common to all areas before comparison.

Tests performed included an overall test for coincidental regression, Newman-Keuls multiple range tests on the slopes of the lines, and multiple range tests for equality of the intercepts of those relationships found to have equal slopes. The procedures outlined in Zar (1974) were followed for all of these tests. If the tests indicated that the relationship under examination did not differ significantly between two or more areas, the data from the areas were combined and a curve fitted to the new set of data using the nonlinear procedure.

Histological Analysis

The ovaries of walleye pollock collected for histological analysis were classified by area, following the same geographic scheme used for the length-at-age and fecundity analyses. The collection was subsampled to obtain ovaries in a complete range of development from each of the five geographic areas. Sections were removed from the central portion of the ovaries. Tanino et al. (1959) have shown that there is no difference in the size composition of oocytes throughout walleye pollock ovaries. All sections were 6 to 10 μm in thickness and were stained with Mayer's haemotoxylin and eosin. In all, 122 ovaries were examined histologically.

Oocytes were classified into 12 categories of development (Hinckley 1986). The overall maturity of each ovary was based on the most advanced oocytes present, and each ovary was assigned to one of 10 maturity classes (Hinckley 1986).

Egg-stage frequency counts, as determined from the histological slides, were used to examine the process of oocyte development. A transect grid was drawn on each slide, and oocyte counts for each stage of development were made at each intersection on the grid. Stage 8 (tertiary yolk) and

stage 9 (nuclear migration) oocytes were called stage 8; stage 11 (maturation) and stage 12 (ovulation) were called stage 11, owing to the difficulty in consistently differentiating these stages. Counts from all points on the grid were combined into a total egg-stage frequency for each ovary. Development of the maturing oocytes could be followed by comparing the egg-stage frequencies for each level of maturity.

Slides were also examined for evidence of ovarian rematuration. Rematuring ovaries were defined as those containing identifiable postovulatory follicles (the remnant of the egg membrane left after ovulation and release of the oocyte); thick ovarian walls; and resorbing, unspawned, fully yolked oocytes in ovaries that also contained vitellogenic oocytes.

RESULTS

Spatial and Temporal Distribution of Spawning

Observer information showed that walleye pollock spawning in the Bering Sea began in the Aleutian Basin in January. As the year progressed, spawning was observed further inward over the continental slope and shelf (Fig. 2A through 2H). Spawning occurred between January and March in the basin, between March and June over the southeastern Bering Sea slope and shelf, and between June and August over the northwest slope and shelf. Scattered spawning was noted in the northwestern areas as late as October.

Spawning walleye pollock were caught at depths ranging from 46 to 360 m, most commonly between 100 and 250 m. Temperatures at these depths ranged from $-1.8°$ to 6.0°C ($\bar{x} = 2.34$°C).

The monthly distribution of the commercial fishing fleet in the Bering Sea was examined to assess whether observer reports from the fleet represented the true distribution of spawning. If significant portions of the Bering Sea were not fished by the fleet, concentrations of spawning walleye pollock could have been missed. In January and February, coverage of the continental shelf was scattered and in May most fishing occurred in the southeast portion of the Bering Sea. Coverage of the Aleutian Basin was minimal after March because harvestable concentrations of spawning walleye pollock could not be found in the area after this time (R. Nelson[5]). Nevertheless, the fishing fleet distribution appears to have been sufficiently extensive to detect the majority of spawning walleye pollock, and the reports of spawning obtained from the fleet appear to reasonably represent the true spawning distribution for 1984.

Length-Age Characteristics of Walleye Pollock from Spawning Concentrations

The plots of mean length at age for walleye pollock males (Fig. 3) and females (Fig. 4) suggest that length at age was similar for both sexes in the Aleutian Basin and over the northwest slope. Lengths for the older ages were smaller in these areas than in the other three. Although the data were widely scattered, length at age was similar in the southeast shelf, southeast slope, and northwest shelf, and was larger in these areas than in the basin and the northwest slope.

Comparison of the length-at-age data from $\frac{1}{2}°$ by 1° cells with the growth curves generated by Francis and Hollowed showed that most of the cells assigned to the "northern" group were in the northern slope and buffer areas and in the Aleutian Basin (Fig. 5). Walleye pollock in these areas were characterized by a smaller mean length at age. Cells designated as "southern" were mostly from the southeast and northwest shelf areas and southeast buffer zone (Fig. 5) and contained walleye pollock with a larger mean length at age. The spawning concentrations of walleye pollock, therefore, show the same geographic distribution of the two growth types as seen by Lynde et al. (fn. 2) and Francis and Hollowed (unpubl. data).

Length-Fecundity Relationship

In all areas of the Bering Sea, the length-fecundity relationship for walleye pollock (Fig. 6) was found to be curvilinear ($F = aL^b$, Table 1), similar to that observed for walleye pollock from other regions. The overall test for coincidental regression indicated ($F = 5.51$, $P < 0.001$) that the length-fecundity relationships for the four areas were not identical.

Multiple range test results (Table 2) indicated that the northwest and southeast shelf and slope area regression slopes did not differ significantly.

[5]R. Nelson, Observer Program, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

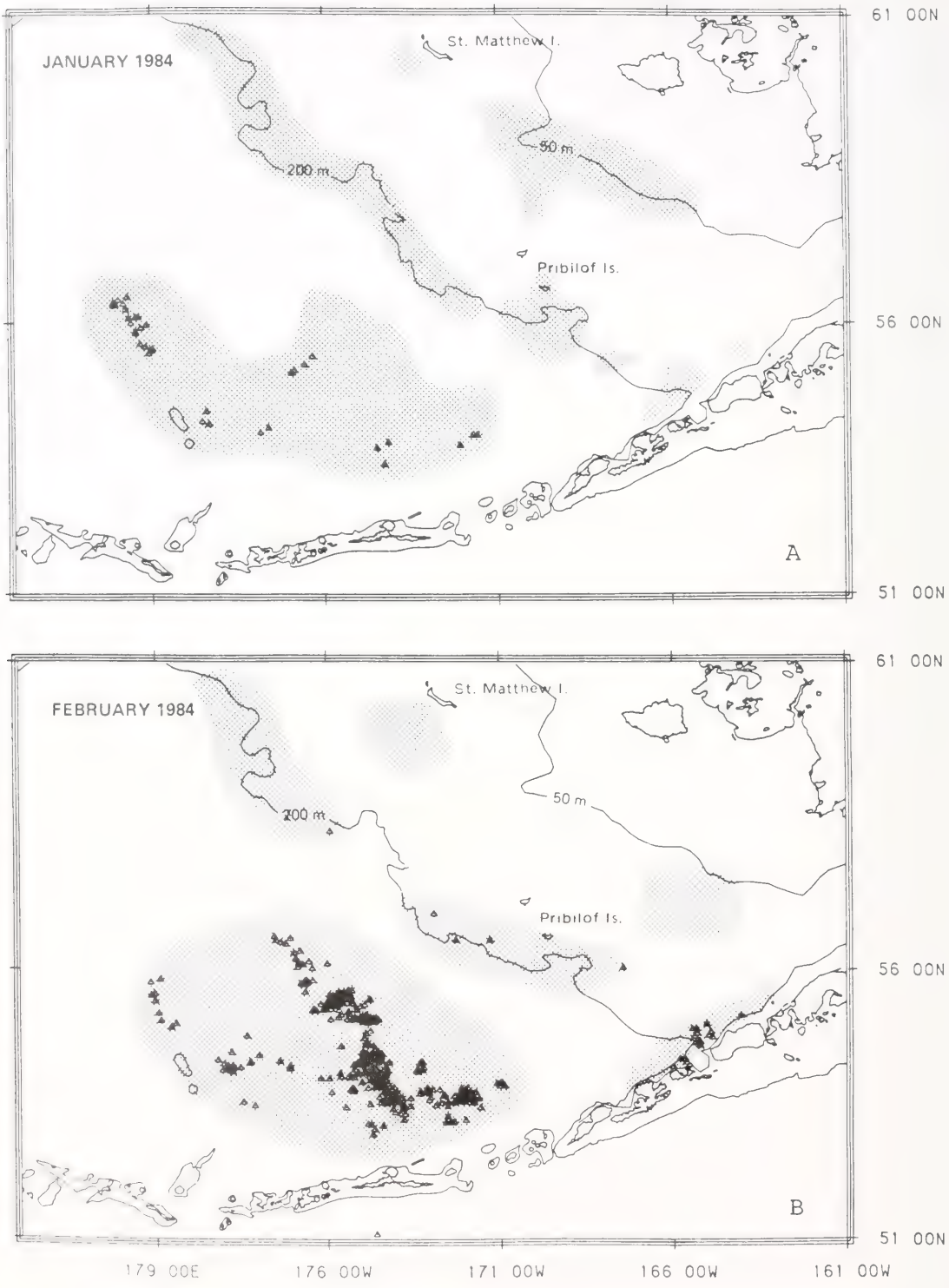


FIGURE 2.—Observed distribution of spawning walleye pollock in 1984, by month. Shaded areas indicate distribution of the

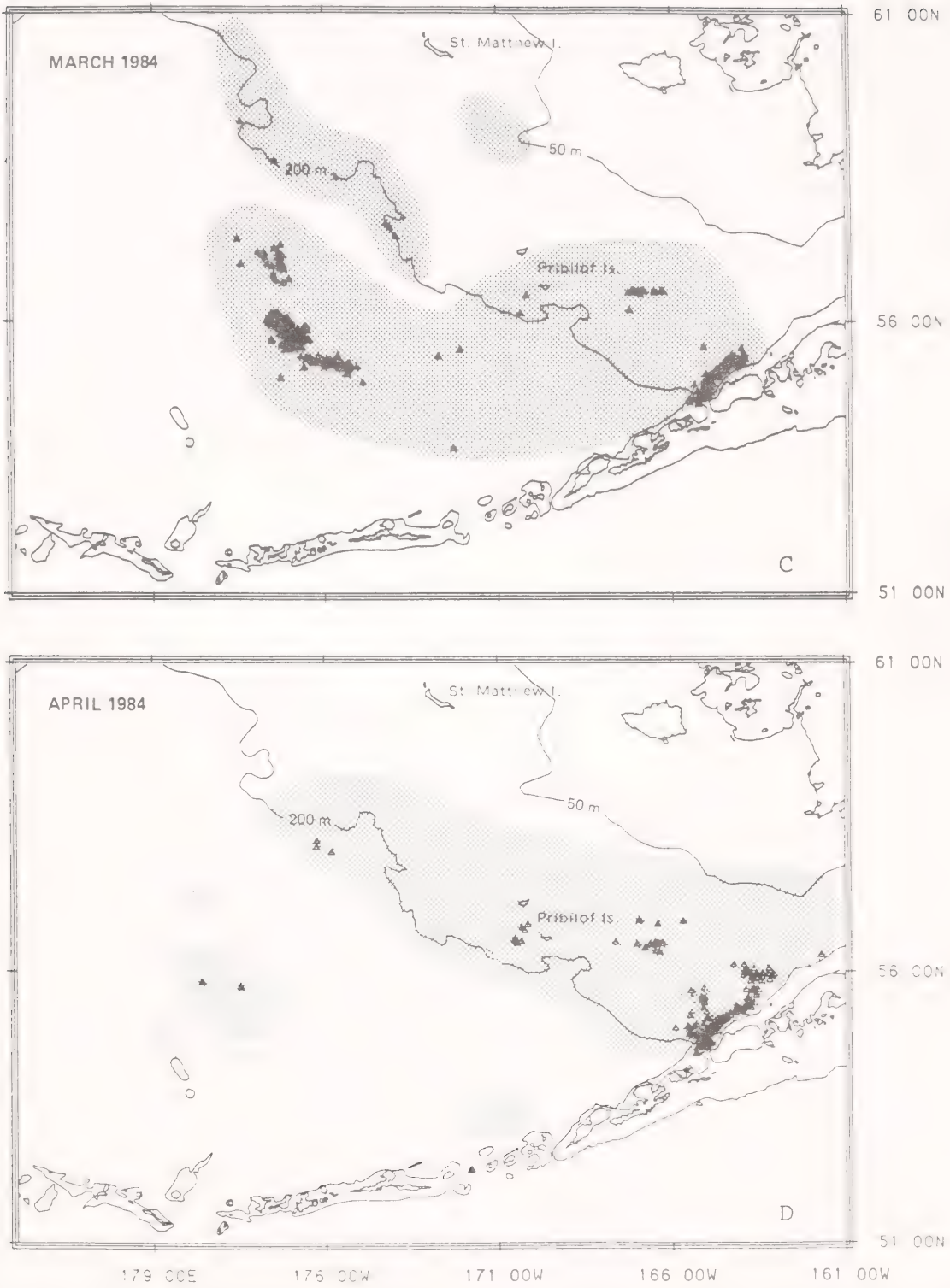


FIGURE 2.—*Continued*—foreign commercial fishing fleet. Triangles indicate hauls in which spawning walleye pollock were caught.

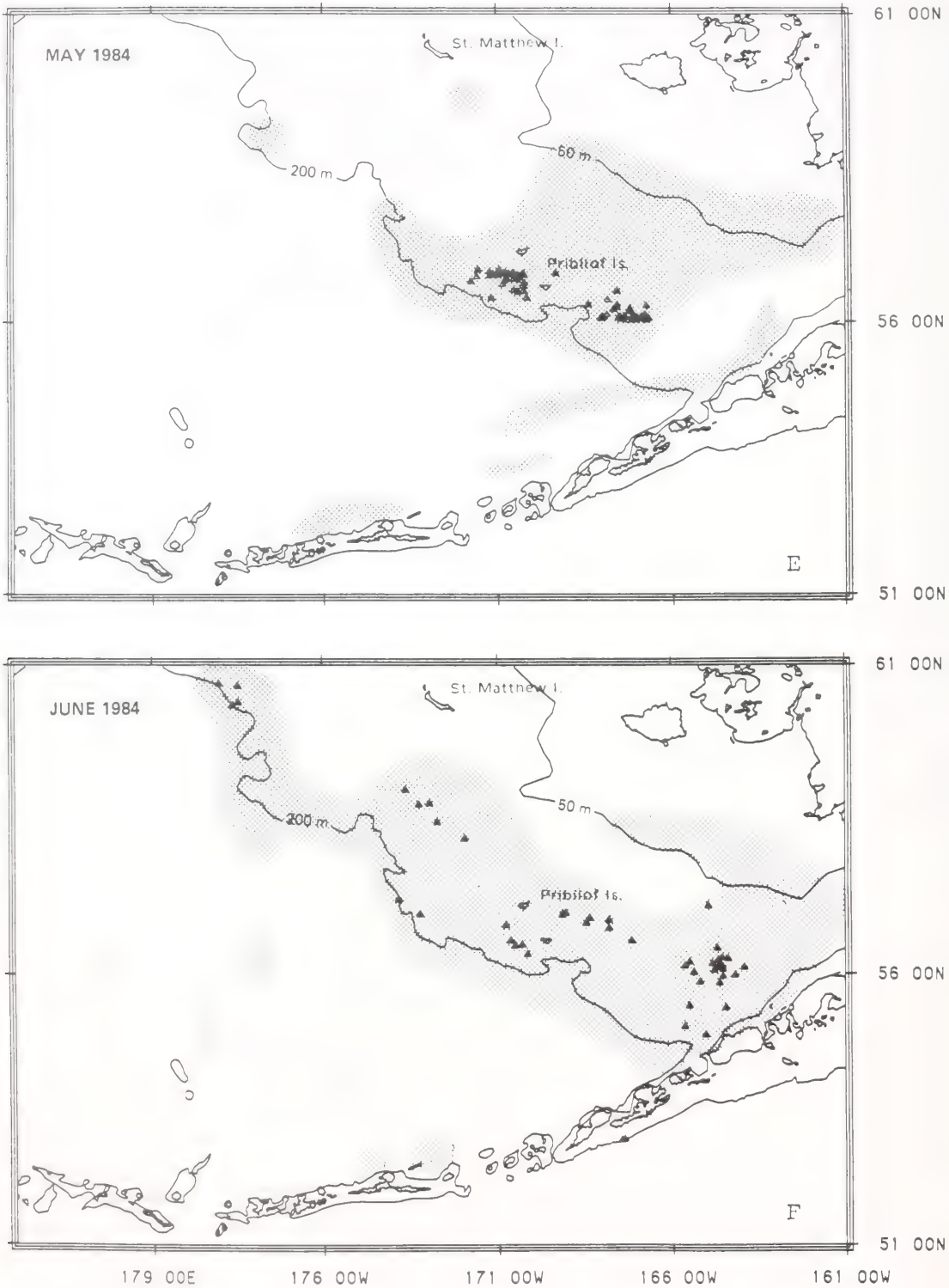
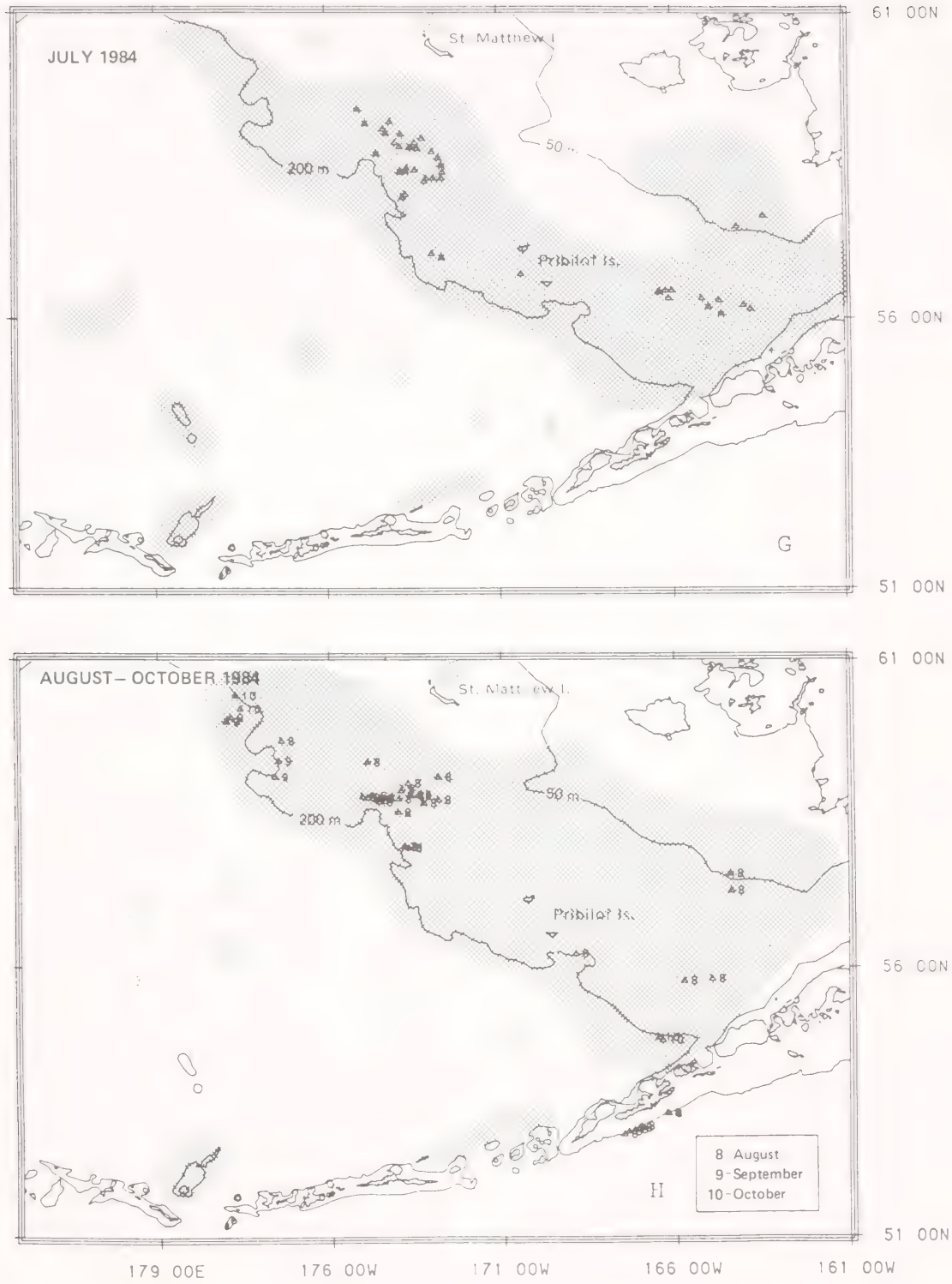


FIGURE 2.—*Continued.*



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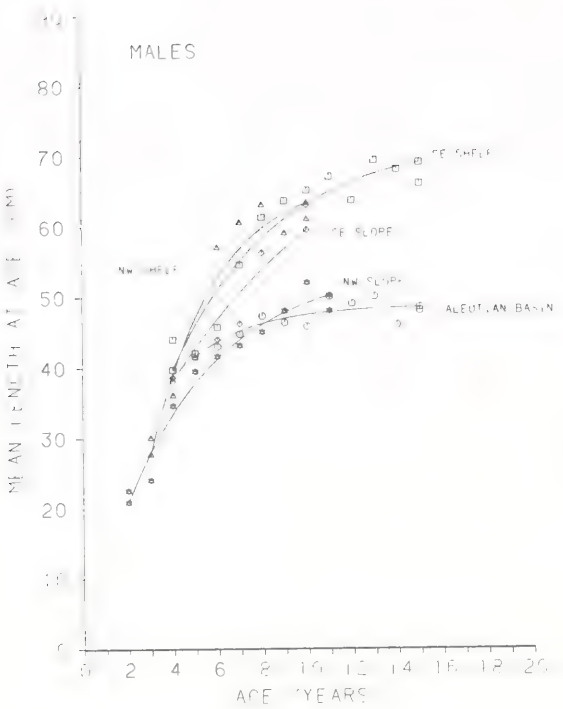

FIGURE 3.—Mean length at age for male walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

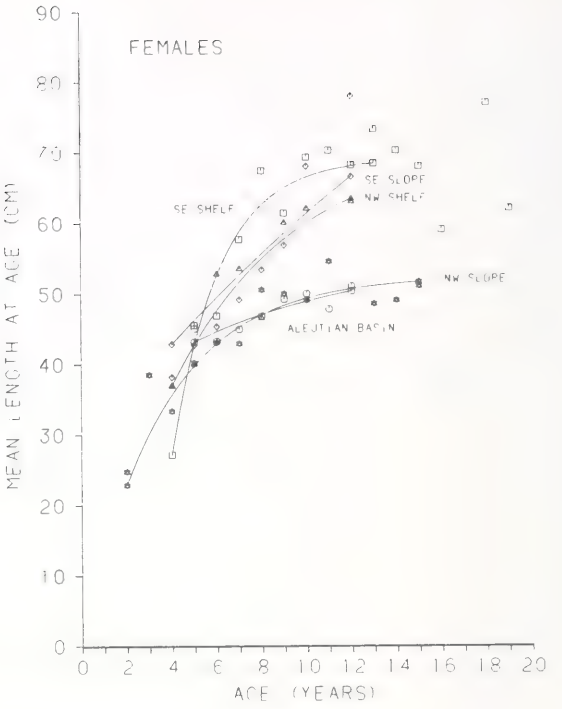

FIGURE 4.—Mean length at age for female walleye pollock from spawning concentrations in five areas of the Bering Sea. Squares indicate fish from the southeast shelf area; triangles, fish from the northwest shelf area; diamonds, fish from the southeast slope area; stars, fish from the northwest slope area; and circles, fish from the Aleutian Basin.

TABLE 1.—Length, weight (W), and fecundity (F) relationships for Bering Sea walleye pollock resulting from the nonlinear regression.

		Length-fecundity		Length-weight		Weight-fecundity	
Region	n	F	R^2	W	R^2	F	R^2
Southeast shelf	25	$0.1926L^{3.5439}$	0.865	$0.0120L^{2.8744}$	0.996	$91.7096W^{1.1423}$	0.877
Aleutian Basin	20	$469.2282L^{1.5575}$	0.769	$0.1257L^{2.2300}$	0.983	$9{,}119.3100W^{0.4570}$	0.737
Southeast slope	28	$4.6528L^{2.8066}$	0.944	$0.0041L^{3.1134}$	0.997	$906.4315W^{0.8534}$	0.935
Northwest slope	38	$0.0872L^{3.7869}$	0.995	$0.0001L^{3.4862}$	0.999	$118.6879W^{1.1439}$	0.995
Combined areas	91	$^{1}0.1719L^{3.6046}$	0.907	$^{2}0.0027L^{3.2743}$	0.996	$^{1}174.9222W^{1.0765}$	0.900

The multiple range test on the regression intercepts could not distinguish the intercepts of the three lines from the slope and shelf areas. The multiple range test on regression slopes also showed that the slopes of the regressions from the Aleutian Basin and from the southeast slope areas could not be distinguished; however, the intercepts of the regressions from these two areas differed significantly.

Based on these analyses, the length-fecundity relationships from all shelf and slope areas appeared to be similar, and the relationship in these areas was different from that seen in the Aleutian Basin. Fecundity increased almost linearly with length in Aleutian Basin walleye pollock; however, pollock larger than about 60 cm are not found in the basin (Okada 1977[6], 1983[7]; J.

[6]Okada, K. 1977. Preliminary report of an acoustic survey of the pollock stock in the Aleutian Basin and the adjacent waters in the summer of 1977. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, September 1977. Fishery Agency of Japan.

[7]Okada, K. 1983. Biological characteristics and abundance of the pelagic pollock in the Aleutian Basin. Document

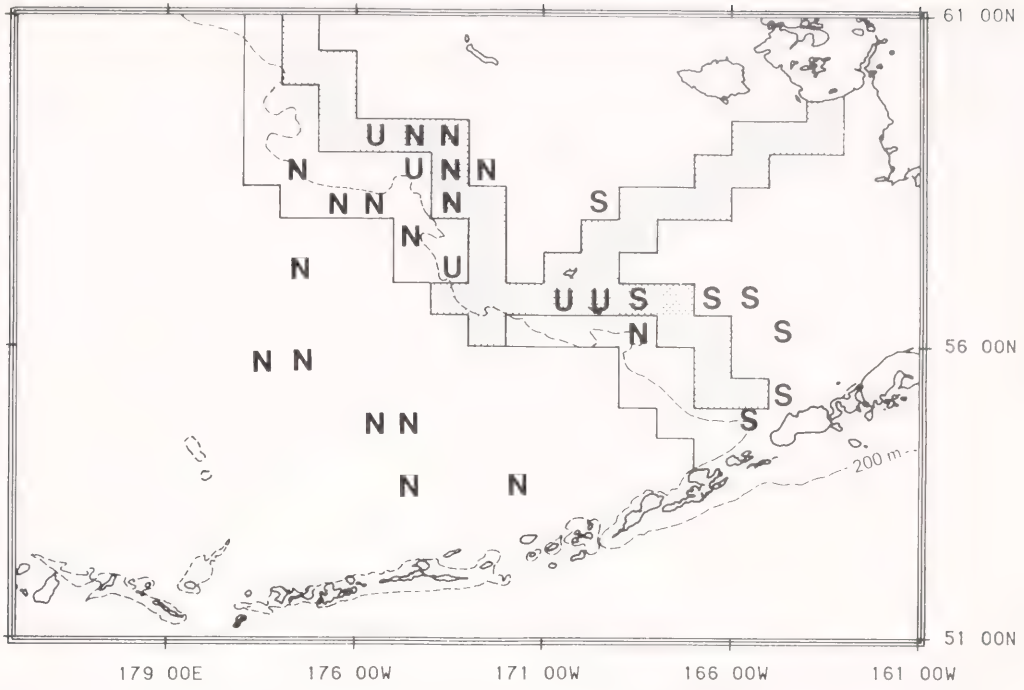

FIGURE 5.—Locations of cells containing walleye pollock from spawning concentrations with growth rates similar to "northern" (N), "southern" (S), or "unknown" (U) groups of Lynde et al. (text footnote 2).

Traynor[8]). The great increase in fecundity, seen in fish larger than 60 cm, resulted in the observed curvilinear relationships found in the other areas.

Length-Weight Relationship

The multiple range test results on the length-weight relationship for walleye pollock were inconclusive (Table 3). The hypothesis that the length-weight relationship was the same in all areas was rejected ($F = 3.4156$, $0.0025 < P < 0.005$), but the slopes of the regression lines did not differ significantly. A test of intercept equal-

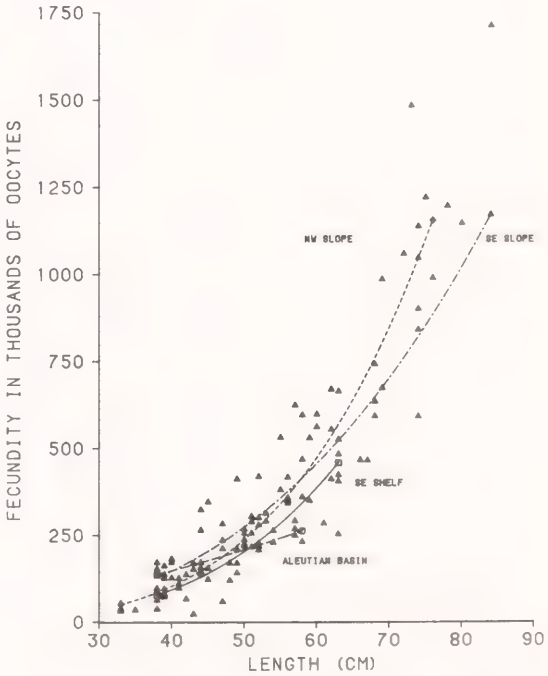

FIGURE 6.—Observed and predicted relationships between fecundity and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

submitted to the annual meeting of the International North Pacific Fisheries Commission, 1983. Far Seas Fisheries Research Laboratory, Japan.

[8]J. Traynor, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. 1984.

TABLE 2.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-fecundity regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	1.6554	2.7661	4.0967	4.2659
Area:	Aleutian Basin	SE slope	SE shelf	NW slope

Comparison	Difference	SE	q	p	q(0.05,78,p)
4 vs. 1	2.6105	0.5320	4.9070	4	3.70
4 vs. 2	1.4998	0.5735	2.6152	3	3.37
4 vs. 3	Do not test				
3 vs. 1	2.4413	0.4926	4.9559	3	3.37
3 vs. 2	Do not test				
2 vs. 1	1.1107	0.5928	1.8737	2	2.81

INTERCEPTS

A.

Ranks of intercepts:	1	2	3
Ranked intercepts:	−4.211	−3.864	1.711
Area:	NW slope	SE shelf	SE slope

Comparison	q	p	q(0.05,60,p)
3 vs. 1	1.3870	3	3.40

B.

Ranks of intercepts:	1	2
Ranked intercepts:	1.711	5.784
Area:	SE slope	Aleutian Basin

Comparison	q	p	q(0.05,35,p)
2 vs. 1	3.6720	2	2.88

TABLE 3.—Newman-Keuls multiple range tests on the slopes and intercepts of the linearized length-weight regressions from four areas in the Bering Sea (following the notation of Zar 1974).

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	2.7927	2.8883	3.1635	3.3161
Area:	Aleutian Basin	SE shelf	SE slope	NW slope

Comparison	Difference	SE	q	p	q(0.05,107,p)
4 vs. 1	0.5234	1.7581	0.2977	4	3.70

INTERCEPTS

Ranks of intercepts:	1	2	3	4
Ranked intercepts:	−6.3145	−5.6965	−4.5605	−4.1570
Area:	NW slope	SE slope	SE shelf	Aleutian Basin

Comparison	q	p	q(0.05,107,p)
4 vs. 1	6.2685	4	3.70
4 vs. 2	4.1848	3	3.37
4 vs. 3	1.4944	2	2.81
3 vs. 1	4.3880	3	3.37
3 vs. 2	2.5906	2	2.81
2 vs. 1	0.4340	2	2.81

ity showed a significant difference ($F = 3.608$, $0.01 < P < 0.025$); however, the multiple range test on intercepts was inconclusive and showed overlaps in the equality of intercepts by area. The curves in Figure 7 all appear similar. A nonlinear regression on the combined data from all areas explained a high percentage of the overall variation (99.63%) (Table 1). It seems reasonable to use one equation to describe the length-weight relationship for all areas combined.

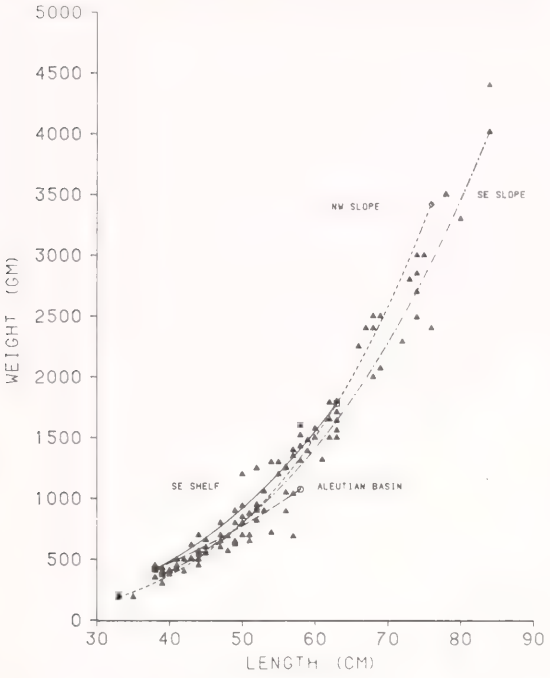

FIGURE 7.—Observed and predicted relationships between weight and length for walleye pollock from four areas within the Bering Sea. Triangles indicate the weight of the sampled fish.

Weight-Fecundity Relationship

The weight-fecundity relationship for walleye pollock in all areas was nearly linear (Fig. 8). The overall test for coincidental regressions indicated that the weight-fecundity relationship differed significantly between areas ($F = 7.6534$, $P < 0.001$). Comparison of the linearized equations showed that the regression slopes were similar in the northwest continental slope, the southeast continental shelf, and the southeast continental slope areas (Table 4). The multiple range test on the intercepts of the regressions from the two continental slope areas indicated that they were similar, but different from the regression intercept of the line from the southeast shelf area. The multiple range test on the regression slopes showed that the slope of the weight-fecundity regression for Aleutian Basin pollock was similar to that seen in the southeast continental slope area; however, a comparison of the intercepts did show a significant difference between these two areas.

As with the length-fecundity relationship, the weight-fecundity relationship appeared similar in the continental shelf and slope areas, and differed from the relationship seen in the Aleutian Basin. The weight-fecundity relationship for the Aleutian Basin showed the same trend that was seen for length-fecundity, i.e., a much more gradual increase in fecundity with weight than in other areas.

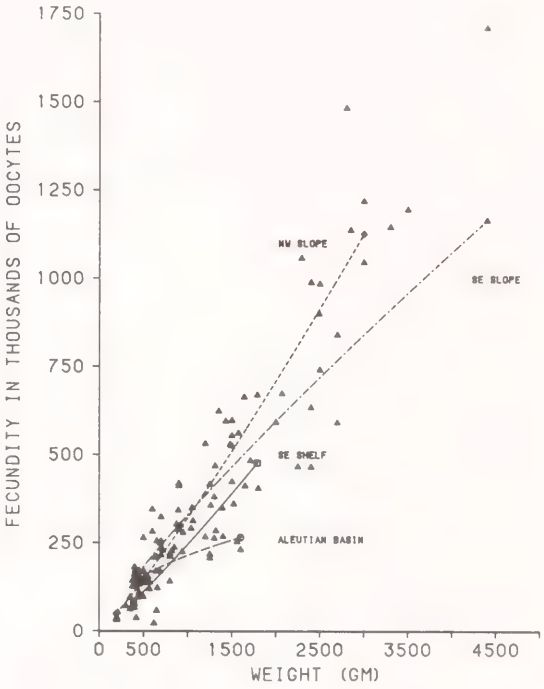

FIGURE 8.—Observed and predicted relationships between fecundity and weight for walleye pollock from four areas within the Bering Sea. Triangles indicate the number of oocytes per sampled fish.

Ovarian Maturation

Examination of the egg-stage frequencies indicates that the process of ovarian development in Bering Sea walleye pollock (Fig. 9A through 9M) is one of partial synchrony. A "reserve" fund (Foucher and Beamish 1980) of small, unyolked oocytes exists at all times in the ovary; this consists of oocytes at the early and late perinucleus stages. The reserve fund is represented by the single mode in Figure 9A. A portion of this group begins the process of yolk formation, advancing asynchronously to the fully yolked tertiary yolk stage (stage 8). This developing mode is visible in Figure 9B, C, and D. When vitellogenesis is complete, the mode of developing oocytes is com-

TABLE 4.—Newman-Keuls multiple range tests on the slopes and intercepts of the the notation

SLOPES

Ranks of slopes:	1	2	3	4
Ranked slopes:	0.5169	0.9577	1.2280	1.3978
Area:	Aleutian Basin	SE slope	NW slope	SE shelf

Comparison	Difference	SE	q	p	q (0.05,78,p)
4 vs. 1	0.8809	0.1555	5.6650	4	3.70
4 vs. 2	0.4401	0.1698	2.5919	3	3.37
4 vs. 3	Do not test				
3 vs. 1	0.7111	0.1574	4.5178	3	3.37
3 vs. 2	Do not test				
2 vs. 1	0.4408	0.1847	2.3866	2	2.81

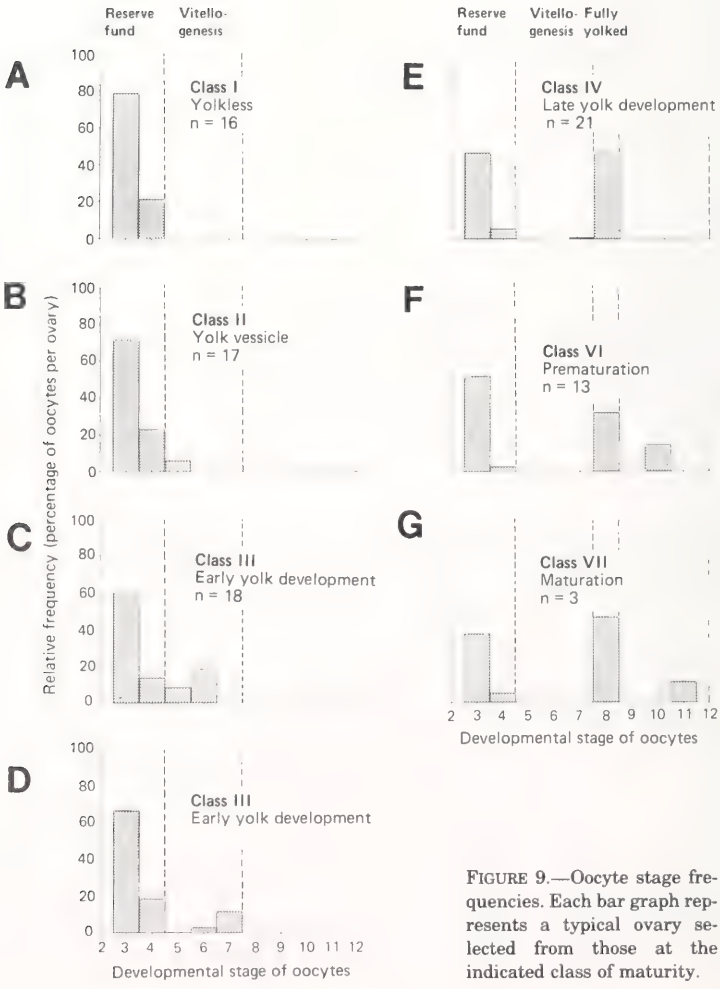

FIGURE 9.—Oocyte stage frequencies. Each bar graph represents a typical ovary selected from those at the indicated class of maturity.

inearized weight-fecundity regressions from four areas in the Bering Sea (following of Zar 1974).

INTERCEPTS

A. Ranks of intercepts:	1	2	3
Ranked intercepts:	2.7420	4.2815	6.1588
Area:	SE shelf	NW slope	SE slope

Comparison	q	p	q(0.05,60,p)
3 vs. 1	6.4957	3	3.40
3 vs. 2	1.3520	2	2.83
2 vs. 1	5.4330	2	2.83

B. Ranks of intercepts:	1	2
Ranked intercepts:	6.1588	8.7805
Area:	SE slope	Aleutian Basin

Comparison	q	p	q(0.05,35,p)
2 vs. 1	5.2249	2	2.88

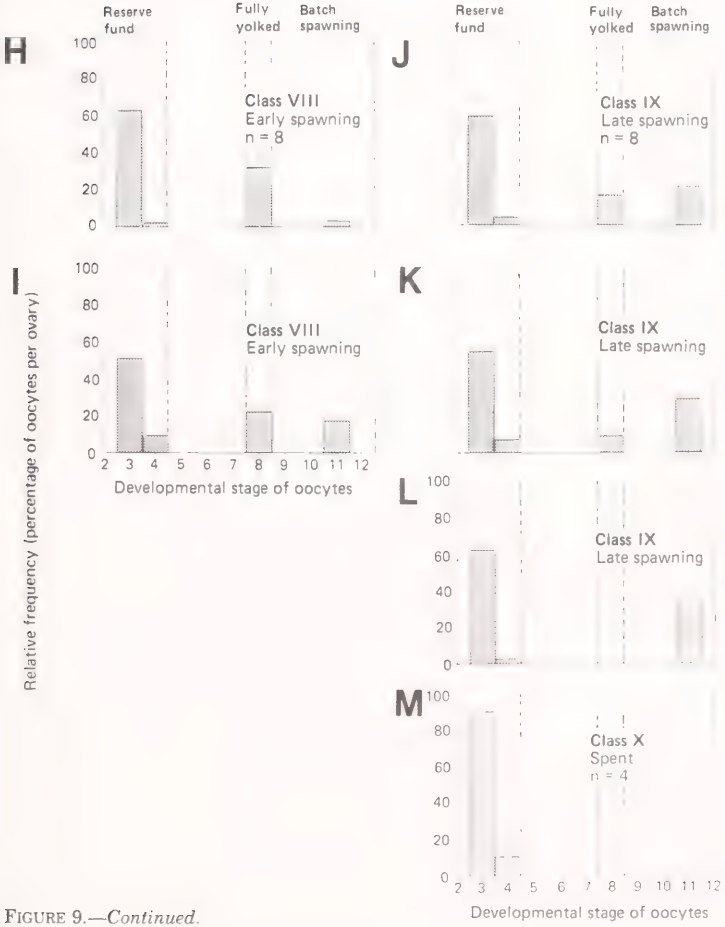

FIGURE 9.—*Continued.*

pletely separated from the remaining reserve fund (Fig. 9E). This appears to be the best stage to estimate fecundity, as no more eggs will be recruited into the developing mode, and spawning has not yet begun.

The final part of the maturation process appears to occur in a synchronized manner, with successive groups of fully yolked oocytes proceeding through the last stages (homogenization of yolk, hydration, ovulation, and release) in discrete batches. During the spawning period, the proportion of nonhydrated (stage 8) oocytes gradually decreases, and that of hydrated oocytes (stage 11) increases, until only hydrated oocytes remain. This progression is visible in Figure 9H through L. The spawning of matured oocytes in discrete groups appears to represent the "batch spawning" process in walleye pollock.

Spent ovaries contain oocytes in the early and late perinucleus stages (the reserve fund), postovulatory follicles, and, in some cases, yolked but unspawned oocytes undergoing resorption. Redeveloping ovaries, i.e., those containing signs of prior spawning and vitellogenic oocytes, were found in small numbers (9 out of 122 ovaries examined). Of the 18 ovaries examined for March, only one appeared to be developing new oocytes, possibly early enough for a second spawning that year. The rest of the redeveloping ovaries were collected from June to September from walleye pollock in the southeast shelf area. Redeveloped ovaries found in the summer with oocytes at the yolk vessicle stage may spawn in the autumn or during the next year (small numbers of walleye pollock have been observed in spawning condition throughout the year). Rematuring ovaries containing oocytes at the primary and secondary yolk stages were found only in August and September. More than one-half of these ovaries (5 out of 8) showed signs of resorption of the developing oocytes, and would probably not spawn again that year.

DISCUSSION

The results of this study appear to indicate that at least three separate spawning stocks of walleye pollock exist in the Bering Sea. One is located in the Aleutian Basin, a second over the northwest continental slope, and a third in the southeast shelf, southeast slope, and northwest shelf areas.

As noted by Ogawa (1956), geographical isolation or ecological separation of spawning concentrations may indicate population separation. Overall, the spawning season in the Bering Sea lasts about 8 months, and spawning within the different areas is separated by 500 to 1,000 km. Within the different areas, spawning lasts 2 to 3 months.

Dissimilarities in several population characteristics were observed between groups spawning in the different areas, supporting the concept of multiple stocks. Length at age differed by area, with larger length at age seen in walleye pollock spawning over the southeast shelf, southeast slope, and northwest shelf, and smaller length at age seen in walleye pollock spawning in the Aleutian Basin and over the northwest slope. These results were also found by Lynde et al. (fn. 2).

Fecundity relationships in all shelf and slope areas were similar, and differed from that seen in the Aleutian Basin. Aleutian Basin walleye pollock showed the lowest fecundity. Walleye pollock from the northwest and the southeast slope areas showed the highest fecundity. Fecundity estimates for walleye pollock in Shelikof Strait in 1982 (Miller et al. 1986[9]; $F = 1.2604L^{3.2169}$) and in British Columbia waters in 1979 (Thompson 1981; $F = 6.771L^{2.981}$) are higher than the Bering Sea estimates from this study. A general trend of declining fecundity exists towards the northern range of walleye pollock. Due to possible interannual variability in fecundity, caution should be taken in comparing studies done in different regions and years.

Further research is needed for walleye pollock, in the Bering Sea and elsewhere, to determine the proportion of annual fecundity actually realized, i.e., whether resorption of yolked oocytes during maturation and after spawning is significant. Preliminary histological analysis of walleye pollock ovaries from Shelikof Strait (Hinckley unpubl. data) suggests that resorption of yolked oocytes may not be significant.

Based on similarities in growth, Lynde et al. (fn. 2) proposed that mixing of walleye pollock stocks occurs between the Aleutian Basin and the northwest slope; however, the findings of this study indicate the mixing does not occur during the spawning season. Spawning over the basin and the northwest slope is separated by about 5 months and 500 km, yet there was no sign of

[9]Miller, B. S., D. R. Gunderson, D. Glass, D. B. Powell, and B. A. Megrey. 1986. Fecundity of walleye pollock (*Theragra chalcogramma*) from Shelikof Strait, Gulf of Alaska. Fish. Res. Inst. Rep. FRI-UW-8608. Univ. Washington, Seattle, WA 98195.

rematuration in walleye pollock ovaries collected from the northwest slope late in the season, which could have indicated that these fish spawned first in the basin and then later on the northwest slope. The difference in fecundity between these areas also supports the theory that spawners found in the northwest slope area form a separate group from those found in the Aleutian Basin. The similarities in growth found by Lynde et al. (fn. 2) may be a result of mixing occurring at other times of the year.

A reduced food supply may produce the smaller length at age and lower fecundity of Aleutian Basin walleye pollock. The reduced growth of walleye pollock in the basin is probably due to the lack of fish, particularly juvenile walleye pollock, in the diet (Okada fn. 7; Traynor and Nelson 1985; Dwyer et al. in press). Dwyer (1984) also found that the mean weight of stomach contents of basin-caught fish was low compared with that of fish caught over the shelf and slope. Reduced food supplies have been shown to lower fecundity in several species (Scott 1962; Hester 1964; Bagenal 1969; Leggett and Power 1969; Wootton 1973, 1977; Hislop et al. 1978).

Histological examination of walleye pollock ovaries further supports the theory that spawning concentrations found in widely separated areas do not mix extensively. Walleye pollock spawning in the Bering Sea can be classified as partially synchronous, with one discrete group of oocytes brought to maturation and then spawned in successive batches. This is similar to the process described for walleye pollock from Japan (Sakurai 1977). The maturation of a second group of oocytes from vitellogenesis to spawning within 1 year does not appear to be common. Maximum walleye pollock fecundity is therefore annually determinate, and the duration of an individual female's spawning period is limited by the duration of the batch spawning process. If an individual does batch spawn a group of matured oocytes over 1 month, as Sakurai's (1982) laboratory studies suggest, it seems unlikely that it would migrate any great distance over this time while actively spawning.

To infer stock separation from the results of this study (i.e., that fish return to the same discrete areas each year to spawn) requires assuming that the timing and distribution of spawning, the dynamics of ovarian maturation, and the differences in growth and fecundity remain relatively constant from year to year. The timing and location of spawning have been similar from 1982 to 1986 (Hinckley unpubl. data; R. Nelson fn. 5). The process of maturation is basically the same for walleye pollock found in the Bering Sea, in the Gulf of Alaska (Miller et al. fn. 9), and in Japanese waters (Sakurai 1977, 1982). Differences in mean length at age represent cumulative differences in growth over the life of a fish, and systematic variation by area such as that seen in this study probably reflects separation over a period of years. The study by Lynde et al. (fn. 2) documented the same differences in growth by area over a period of 8 years as was seen in this study for 1984. It is not known at what point annual fecundity is determined in walleye pollock, but as egg production is influenced by food supply in many species, and as walleye pollock feed mostly during the spring and summer and less during the winter (Dwyer et al. 1986) and the spawning season, yearly fecundity may be determined about 1 year before spawning. The results of this study suggest that the assumption of stock separation over a period of years is reasonable.

This study has outlined the timing and distribution of walleye pollock spawning in the Bering Sea for 1984, and postulates the existence of at least three separate spawning stocks. Further research is needed on the biological and oceanographic conditions occurring in the different spawning areas in order to understand the reasons for the apparent separation of stocks, and to clarify differences in recruitment and production by these stocks.

ACKNOWLEDGMENTS

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DISTRIBUTION, FEEDING, AND GROWTH OF LARVAL WALLEYE POLLOCK, *THERAGRA CHALCOGRAMMA*, FROM SHELIKOF STRAIT, GULF OF ALASKA

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ABSTRACT

Walleye pollock in the Gulf of Alaska have recently been found to form an intense spawning aggregation in late winter in Shelikof Strait. This produces a dense patch of planktonic eggs in early April, and later in spring a patch of larvae that can be followed as it drifts to the southwest. The density of larvae observed in 1981 indicated that density-dependent effects on feeding may be important for larval survival. In May 1983 we conducted a field study to investigate spatial and vertical distribution, feeding, and growth of larvae from this spawning. During this study we found, in an area of maximum concentration (~1 larva m^{-3}) located by an initial survey, larvae averaged 11.1 mm SL, and were similar in size to those found elsewhere. The larvae in 1983 were larger, and less abundant than at the same time in 1981. Larval growth was estimated from the number of otolith daily growth increments at size of larva and was similar in the area of maximum concentration and in other areas. Larvae were concentrated vertically between about 15 and 50 m and showed a crepuscular pattern of increased density at 14-28 m during twilight. Neither the vertical nor horizontal patterns of larval occurrences seemed closely associated with particular values of temperature or salinity. Most larvae were found in a temperature range of 7.0°-5.5°C and a salinity range of 31.5-32.2‰. Guts of larvae collected during darkness contained less food than those from daytime. Copepod nauplii were largely replaced by *Pseudocalanus* spp. copepodids in the diet of larvae larger than 14 mm. At the densities of walleye pollock larvae observed in this study, it appears that zooplankton production in the area did not impact larval growth, even in the area of maximum density.

A large spawning concentration of walleye pollock, *Theragra chalcogramma*, was discovered in 1980 in Shelikof Strait, and subsequently a 220,000 metric ton/year fishery developed. Shelikof Strait, a 50 by 200 km body of water in the northern Gulf of Alaska, between the Kodiak Archipelago and the Alaska Peninsula, is apparently the major spawning center for Gulf of Alaska walleye pollock. Ichthyoplankton surveys in 1981 and 1982 showed that spawning occurs primarily in a restricted area within Shelikof Strait and over a short period of time, producing a dense patch of eggs. Thereafter, larvae drift southwest with prevailing currents (Fig. 1). The densities of walleye pollock eggs and early larvae found in Shelikof Strait in 1981 exceeded 50 m^{-3} (Dunn et al. 1984[5]), far greater than their densities in the Bering Sea (Kim and Kendall 1983[6]) or Funka Bay, Japan (Hayashi et al. 1968); moreover, these densities significantly exceed those reported for larvae of any other fish (Hempel 1979).

Energetic requirements of larvae in high densities may exceed production of food and possibly lead to density-dependent effects on larval growth and survival (Jones 1973). At larval densities frequently found (ca. 1 m^{-3}), density-dependent effects are not considered important (McGowen and Miller 1980; Cushing 1983). Laboratory studies, however, have demonstrated effects of stocking

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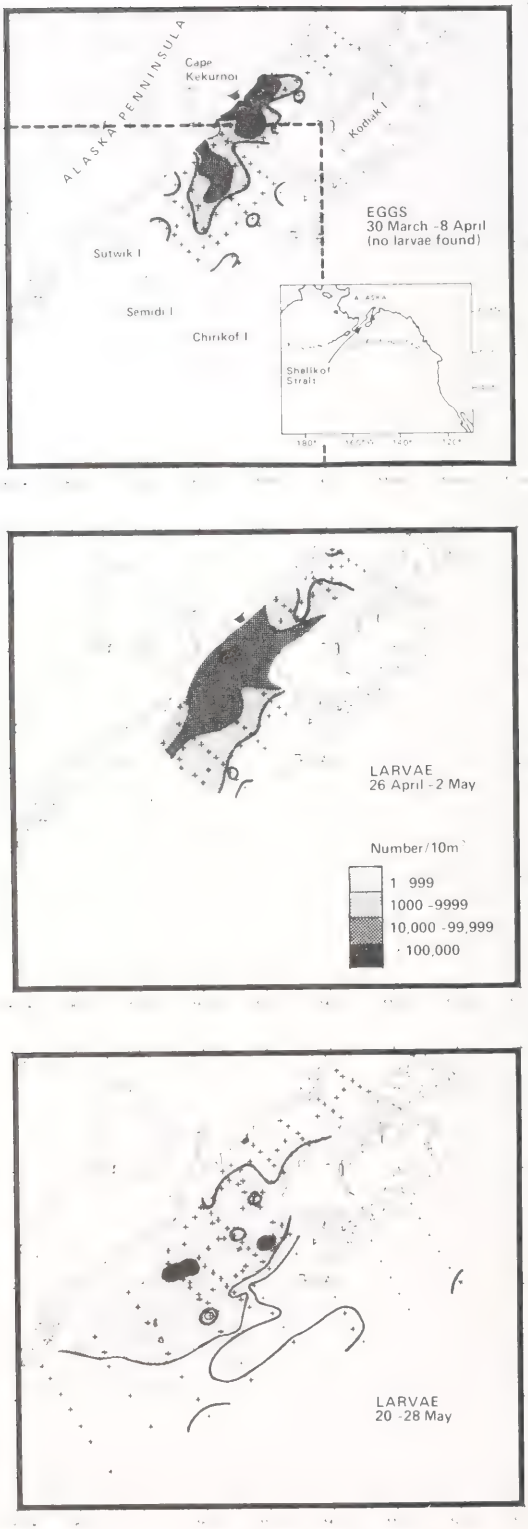

FIGURE 1.—Distribution and abundance of walleye pollock eggs and larvae, spring 1981. Based on Bates and Clark (text fn. 9). Cape Kekurnoi is blackened as a point of reference. Area shown in Figures 2 and 6 is outlined is upper panel.

density upon growth (O'Connell and Raymond 1970; Houde 1975), and recent studies on patches of larvae co-occurring with prey suggest that enhanced growth may be observed at high prey concentrations in the field (Govoni et al. 1985). Search volumes of 5 mm larvae morphologically similar to walleye pollock are about 10 L per day (Laurence 1982); thus with densities of 1 larva in 25 L found in Shelikof Strait in 1981, it is possible that density-dependence is important in larval feeding rate and growth.

Walleye pollock is widely distributed in the subarctic North Pacific. Larval feeding habit studies have been conducted in Uchiura Bay, Hokkaido, Japan (Kamba 1977) and in the southeastern Bering Sea (Clarke 1978) where the principal prey has been found to be copepod nauplii with *Pseudocalanus* spp. becoming increasingly important as the larvae grow. Larval growth in the same areas has been studied by Hayashi et al. (1968) and Nishimura and Yamada (1984) for Hokkaido and by Walline (1985) and Clarke (1984) for the Bering Sea. Growth rates in field collections and laboratory rearing studies have been shown to be quite variable, from about 0.16 to 0.37 mm d^{-1} (Bailey and Stehr 1986).

We conducted a field study to investigate the ecology of larval walleye pollock in Shelikof Strait in May 1983 by locating and sampling the densest patch of larvae. Here we report on growth, feeding habits, and depth distribution of larval walleye pollock we collected.

METHODS AND MATERIALS

Field Collections

An ichthyoplankton survey of 63 stations on a 15 nmi (27.8 km) grid southwest of Kodiak Island, AK, was conducted aboard the NOAA ship *Chapman* from 21 to 28 May 1983 (Fig. 2). At each station a MARMAP double oblique bongo tow (Posgay and Marak 1980) was made from the surface to 200 m (as water depths permitted) with a 60 cm bongo net equipped with 505 μm mesh nets. Flowmeters were mounted in the net mouths and a bathykymograph was used to determine the maximum tow depth and to evaluate the tow profile. A neuston net (Sameoto and Jaroszynski 1969) with 505 μm mesh was also towed for 10 minutes at each station. The neuston net sample and one of the bongo net samples at each station were preserved in 5% sodium borate buffered formalin in seawater. Most walleye pollock larvae from the other bongo net were rough sorted at sea and were immediately preserved in buffered 90% ethanol for otolith examination.

The results of the sorting of larvae at sea were used to choose a location of high larval density for the diel feeding/distribution study (Fig. 2). Another oblique tow, after this survey, confirmed the presence of high concentrations of larvae. Several preliminary tows with four 20 cm bongo nets on the towing wire fixed at 10 m depth intervals (between 5 and 91 m) were made to find depths of maximum larval concentrations. A tow was then taken every 4 hours for 48 hours during 28-30 May 1983 with 20 cm bongo nets equipped with 253 μm mesh nets on one side and 333 μm mesh nets on the other. Four nets were fished simultaneously for 10 minutes at a ship speed of approximately 100 cm/second. The nets were placed on the wire to fish at four depths within the region of larval abundance (nominally 20, 30, 40, and 50 m). Flowmeters were mounted in the mouths of the nets, and a bathykymograph was deployed with the deepest net to record actual tow depths. During setting and retrieving, the ship maintained reduced speed to minimize fishing outside the chosen depth strata. Thus, although no closing devices were used, nearly all of the water passing into the nets was at the chosen depth (Kendall and Naplin 1981). Tows were made at 1030, 1430, 1830, 2330, 0230, and 0630 local time (sunrise was at 0455 and sunset 2138 h). During the sampling of the stations at 1430 and 0230 on both days, a 1 m^2 mechanical Tucker trawl with 505 μm mesh was fished for 10 minutes at 35 m to investigate escapement from the 20 cm bongo nets. Also during the second 24-h period a 60 cm bongo net with 505 μm mesh was fished about 2 m below the deepest 20 cm bongo net to stabilize the wire and allow further catch comparisons.

Expendable bathythermograph (XBT) casts were done at each survey grid station and at the 1430 and 0230 vertical distribution study stations. Conductivity-temperature-depth (CTD) casts (Ocean Data Equipment Corporation[7] Model 302) were made at 15 of the survey grid stations selected to provide three sections across the major southwesterly setting flow field in the area (Fig. 2).

[7]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

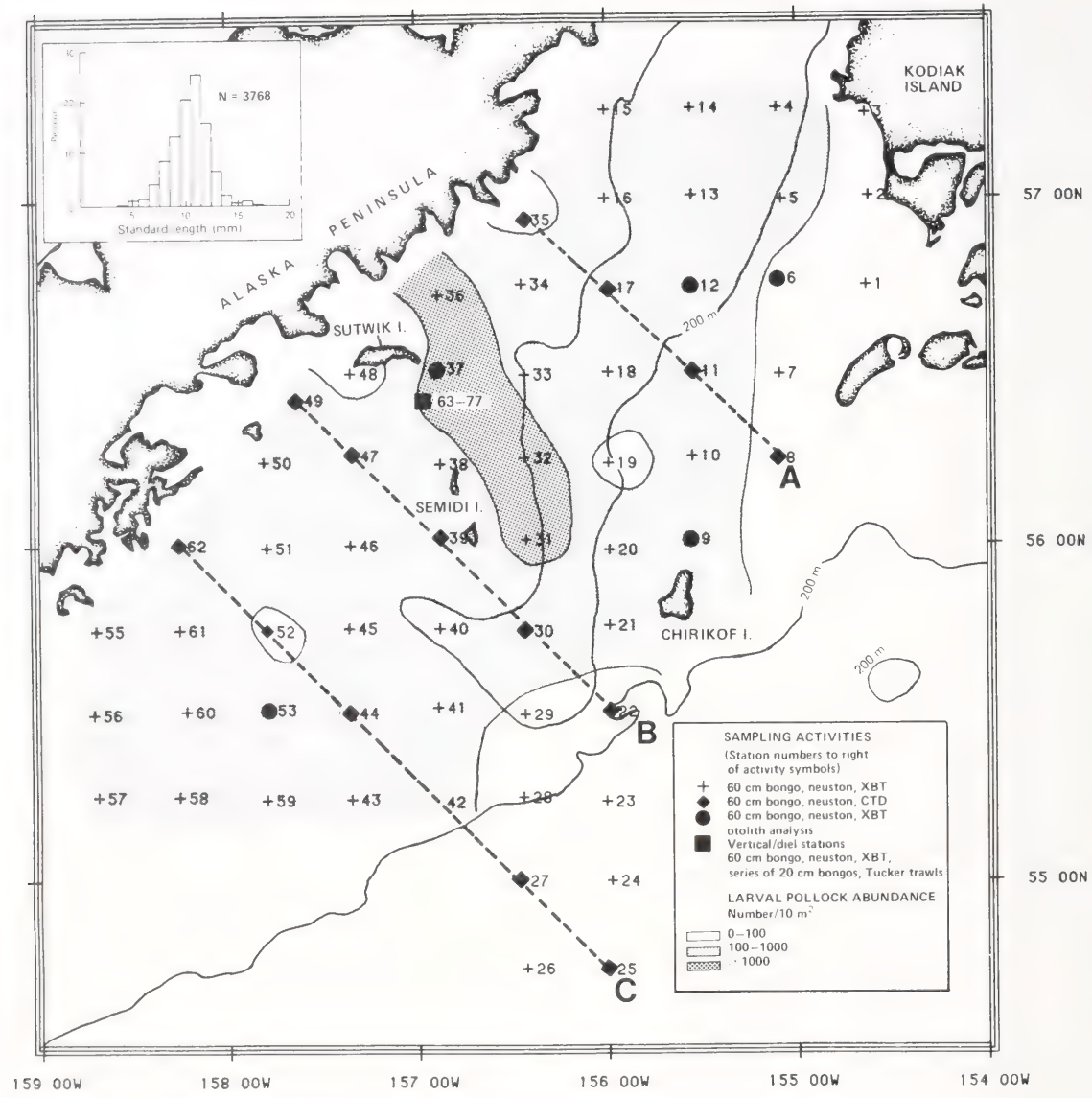

FIGURE 2.—Distribution, abundance (numbers per 10 m^2) and lengths of walleye pollock larvae from 60 cm MARMAP bongo tows superimposed on sampling pattern used in the northern Gulf of Alaska, May 1983. Hydrographic sections are labelled A, B, C (see Figure 4).

Laboratory Procedures

Fish eggs and larvae were identified to the lowest taxon possible at the Polish Plankton Sorting Center in Szczecin, Poland. Fish larvae were measured to the nearst 0.1 mm standard length (SL); when more than 50 larvae of a taxon occurred in a sample, a random subsample of 50 was selected for measurement. Identifications were verified at the Northwest and Alaska Fisheries Center. For distributional analysis of fish eggs and larvae from the survey, numbers per tow for each taxon were converted to numbers under 10 m^2 of water surface using volumes of water filtered and maximum tow depth (see Smith and Richardson 1977). To compare relative abundances of various taxa, an estimate of the total number of eggs or larvae of each taxon present in the entire survey area was derived by summing the catches at each station and multiplying by the

area of sea surface represented by that station (the Sette-Ahlstrom method, see Smith and Richardson 1977). This estimate was thought to make best use of all the available data.

A chi-square test analyzed differences in the numbers of walleye pollock larvae caught as a function of time of day and depth at the diel station. For this test, numbers of larvae in the two sides of the 20 cm bongo nets were combined. Also, catches at the same time and depth but on different days were combined when complete depth series were collected. Four out of six times two complete depth series were collected; at two times only one complete depth series was collected.

Zooplankton were sorted, identified, and enumerated from subsamples of collections made with the 253 μm mesh net. The subsample was chosen such that at least 500 organisms were sorted from each sample.

For larval feeding analysis, 20 walleye pollock larvae (or the total sample when <20 were caught) were selected to represent the size range in the total sample from each of the 333 μm mesh, 20 cm bongo net samples. The guts were dissected from the larvae, and all food items in the foregut, midgut, and hindgut were teased out, identified, and counted.

Lengths and greatest widths were measured for all food items in the larvae collected at 0630, 29 May. Lengths used were carapace length for copepod nauplii, metasome length for copepodids, and total length for all other prey. These measurements were used to estimate volumes of prey organisms, which were applied to the rest of the samples. Mensuration formulae were used to calculate the volume of copepod eggs, copepod nauplii, copepodids of *Pseudocalanus* spp., *Acartia* spp., and *Oithona* spp. (Nishiyama and Hirano 1983; Table 1). *Pseudocalanus* spp. mensuration formulae were used to estimate the volumes of unidentified copepodids. The volumes of other food items were not estimated since their low abundance did not allow adequate measurement of body proportions.

Samples used for age and growth analysis were selected from one station within the area of highest larval density (Station 37, Fig. 2), and from four stations located outside of this dense patch. Standard lengths of larvae from as broad a size range as possible within each sample were measured to the nearest 0.1 mm using an ocular micrometer. Both sagittal otoliths were removed and cleaned using a pair of fine needles under a dissecting microscope fitted with polarizing filters. Whole otoliths were affixed to microscope slides with clear histological mounting medium and increments read in the sagittal plane under a compound microscope with transmitted light at 1000× magnification. Most of the otoliths had a distinct distal-proximal curvature and readability was enhanced when the otolith was mounted with the concave side up.

Increments were identified as a pair of adjacent light and dark bands, formed concentrically around the focus. A prominent dark band surrounding the focus was observed on each otolith (Fig. 3). Since mean otolith diameter at this band (16.0 ± 0.13 μm SE) was similar to the diameter of otoliths from 1-day-old, laboratory-reared larval pollock (18.97 ± 0.37 μm, Nishimura and Yamada 1984; 16-20 μm, Walline 1983; 15.3 ± 1.2

TABLE 1.—Mensuration formulae (Nishiyama and Hirano 1983),[1] length to width ratios, metasome to whole body ratios, metasomal lengths, mean lengths, and mean diameters used to calculate volumes of copepodids, copepod nauplii, and copepod eggs in guts of larval walleye pollock in Shelikof Strait.

Species	K Length:width (this study)	m Metasome:whole body (Nishiyama and Hirano 1983)	Lm Metasomal length (this study)
Pseudocalanus spp.	2.239	0.97	0.870
Oithona spp.	1.824	0.93	0.189
Acartia spp.	3.213	0.95	0.916
Unidentified copepodids	2.539	0.97	0.870

[1]Mensuration formulae (Nishiyama and Hirano 1983):
Volume of copepodids = $[Lm/6 \cdot (Lm/K)^2\pi]/m$.
Volume of copepod nauplii = $\left(\frac{\pi}{24} \text{ carapace length}^3\right)$;
mean carapace length = 0.187.
Volume of copepod eggs = $\left(\frac{\pi}{6} \text{ egg diameter}^3\right)$;
mean egg diameter = 0.110.

μm, Bailey and Stehr[8]), this band was presumed to be the hatching check and was counted as the first increment. Nishimura and Yamada (1984) found that increments were formed daily, beginning with the day of hatching, on the otoliths of laboratory-reared larval pollock. Similar observations have been made on larval walleye pollock otoliths viewed with both light and scanning electron microscopy by Bailey and Stehr (fn. 8). Increments were, therefore, considered to be deposited daily and increment counts were equated with the age of the fish in days after hatching.

The mean of two independent increment counts was used in growth rate analysis. Age-at-length data from each station were fitted separately with simple linear regressions. Analysis of covariance was used to compare growth rates and Dunnett's test of multiple comparisons identified significantly different rates (Zar 1974).

[8]K. Bailey and C. Stehr, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, N.E., Seattle, WA 98115, pers. commun. 7 February 1985.

RESULTS

Hydrographic Observations

Temperature in the survey area varied from just above 7°C at the surface at some stations to slightly <5°C in deeper shelf water (Fig. 4). Temperature gradually decreased with depth, and temperatures in the upper 50 m (where most of the walleye pollock larvae were found) were generally between 7.0° and 5.5°C. At the diel-vertical distribution station, temperatures were similar to those found throughout the area, although the temperature gradient was more uniform than elsewhere. In the upper 60 m at this station, tem-

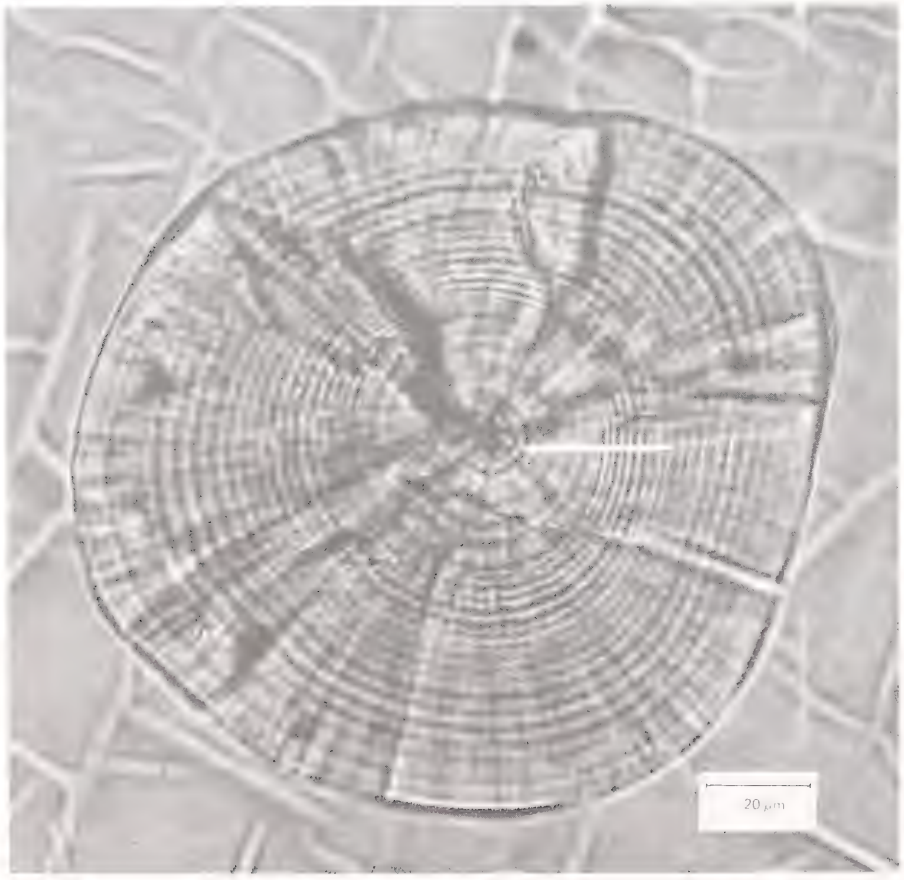

FIGURE 3.—Otolith from a 11.57 mm SL walleye pollock larva showing 27 daily growth increments. The arrow near the focus indicates the first increment. Scale bar indicates 20 μm.

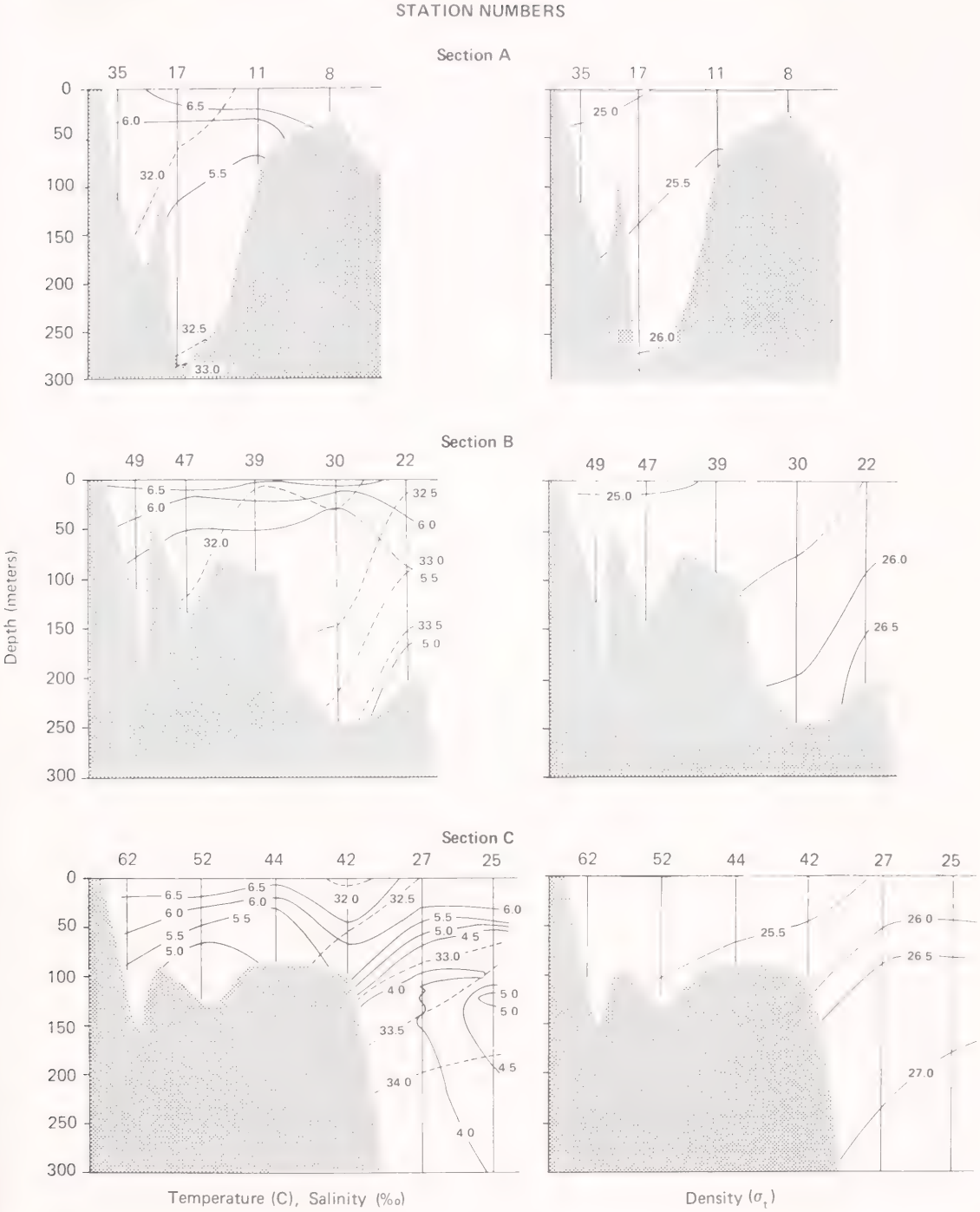

FIGURE 4.—Temperature (solid contours), salinity (broken contours), and density observed in three sections across the sampling area, May 1983. Station and section locations are shown in Figure 2.

perature steadily decreased from 6.9°C to 6.0°C, and at the bottom (120 m) the temperature dropped to 5.5°C. Among the four XBT casts (taken at 12-h intervals), the temperature at a given depth varied as much as 0.5°C: an isotherm depth varied vertically by as much as 50 m.

Salinity varied from 31.5 to >33.5‰ in the survey area. Lowest salinities were found at the surface toward the Alaska Peninsula, and high salinities were found offshore in deeper waters. Isohalines generally sloped from offshore to inshore. This slope was most pronounced at Section A, the one closest to Shelikof Strait. Most larvae were in water between 31.5 and 32.2‰. The salinity profile at the CTD station closest to the diel station showed a slight and steady increase in salinity with depth starting from a surface value of 31.8‰ and ending with a bottom (142 m) value of 32.1‰.

Density sections (σ_t) show the same sloping pattern as the salinity sections but are even more pronounced (Fig. 4). Values ranged from <25.0 at the surface near the Alaska Peninsula to >26.4 in deeper waters near the edge of the continental shelf. No sharp pycnocline was observed but rather a gradual increase in density with depth and distance from the Alaska Peninsula. Most walleye pollock larvae were in water with densities between 25.0 and 25.4 σ_t. The density profile observed near the diel station closely paralleled the salinity profile, with a gradual increase with depth from $\sigma_t = 24.9$ at the surface to $\sigma_t = 25.4$ at the bottom (142 m).

Relative Abundance of Eggs and Larvae

Neuston tows and bongo tows captured eggs of 13 and 14 taxa, respectively (Fig. 5). Rank orders of abundance, based on estimated total numbers of fish eggs in the neuston catches showed *Microstomus pacificus* (Dover sole) to be in greatest abundance, followed by *Glyptocephalus zachirus* (rex sole) and *Theragra chalcogramma*. In bongo catches, unidentified pleuronectid (righteye flounders) eggs were most abundant, followed by those of *M. pacificus, G. zachirus,* and *T. chalcogramma*.

Larvae of 29 and 42 taxa were identified in neuston and bongo catches. Rank order of abundance of fish larvae in neuston tows, based on estimated total numbers, showed *Ammodytes hexapterus* (Pacific sand lance) to be most abundant followed by *Hexagrammos decagrammus* (kelp greenling), *Lyconectes aleutensis* (dwarf wrymouth), *Bathymaster* spp. (ronquils), and *T. chalcogramma*. In bongo catches *T. chalcogramma* larvae were most abundant followed by those of *Bathymaster* spp., *A. hexapterus, Hippoglossoides elassodon* (flathead sole), and unidentified gadids (codfishes).

Distribution and Abundance of Walleye Pollock Eggs and Larvae

Eggs of walleye pollock were taken in 26% of the bongo tows and in 27% of the neuston tows but in low abundance. Only 262 eggs were collected. Some early stage eggs were collected, indicating recent spawning, but older eggs were also present. Eggs were found mainly in water over the deeper part of Shelikof Strait, with decreasing abundance to the southwest (Fig. 6).

Larvae of walleye pollock were found in 89% of the bongo catches and 24% of the neuston catches. The center of larval concentration was near the middle of the survey pattern (Fig. 2). Mean standard length of the larvae throughout the survey was 10.63 mm (range 3.8-21.3 mm, SD = 1.81 mm), with no differences in mean length by area. At each of five stations near Sutwik Island and the Semidi Islands, more than 1,000 larvae/10 m^2 were encountered. At 44 of the 64 stations, more than 100 larvae/10 m^2 were found. A total of over 10^{12} larvae was estimated to be present in the survey area.

Vertical Distribution of Walleye Pollock Larvae

In preliminary tows with the 20 cm bongo nets most larvae were caught above 60 m. During the vertical distribution study actual depths of sampling based on bathykymograph records covered the ranges of 14-20, 21-28, 28-38, and 39-47 m (Table 2).

The mean length of the larvae during our diel vertical distribution study was 11.1 mm SL. The range of mean lengths among the individual samples was 10.0-12.2 mm SL, and the range of standard deviations was 0.8-2.3 among hauls with more than 10 larvae. No patterns of size of larvae with depth or time of day were seen by visual inspection of the data, and since the range of mean lengths was so narrow, and the confidence intervals overlapped, no further analysis was performed.

There were no diel differences in catch rates

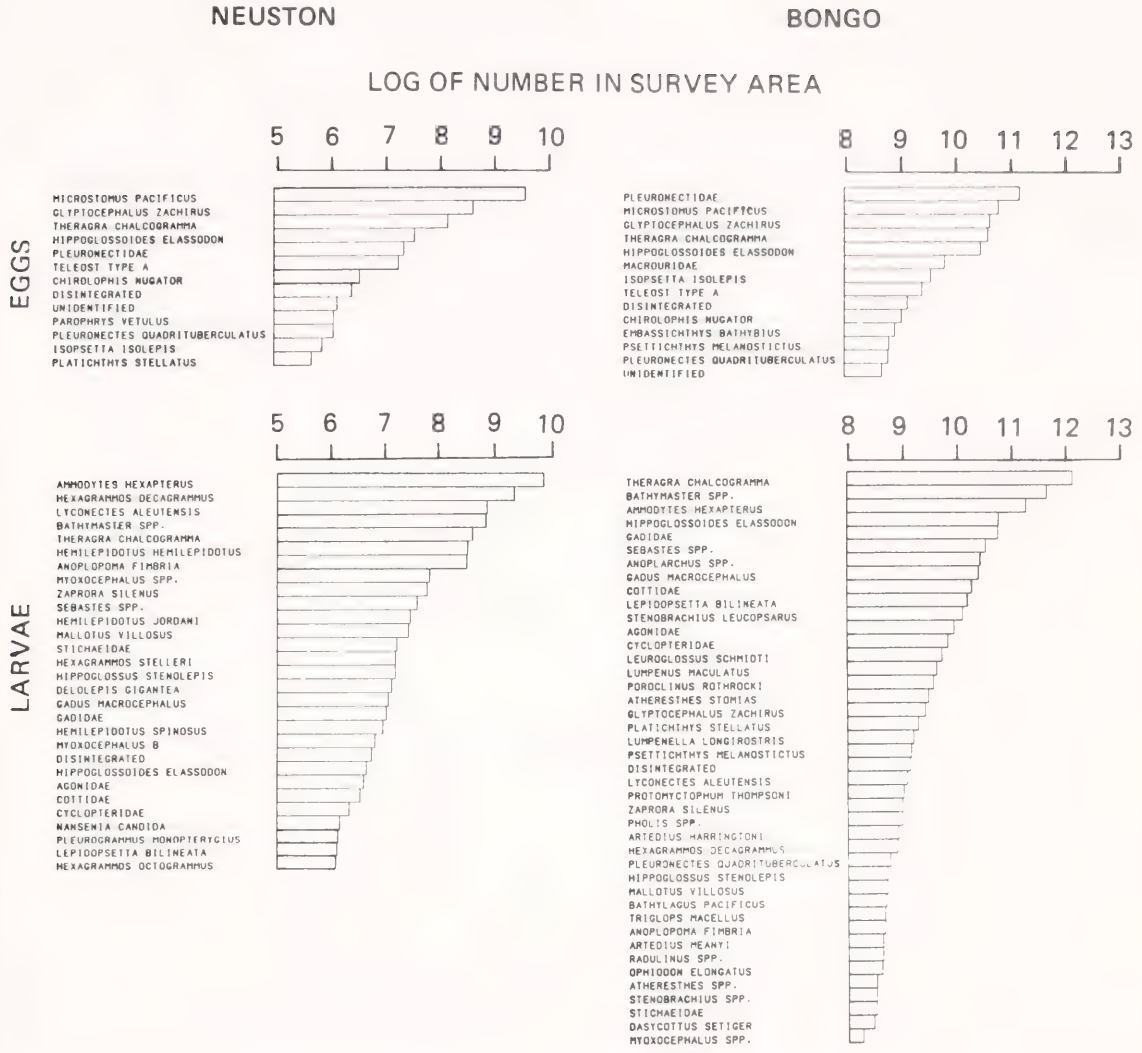

FIGURE 5.—Rank order abundance, as log of total numbers in the survey area, of fish eggs and larvae in neuston and bongo tows during the survey, May 1983.

TABLE 2.—Chi-square test of numbers of walleye pollock larvae with time and depth from the vertical distribution study, May 1983.

	Time											
	1840-1920		2235		0320-0238		0629-0635		1047		1432-1515	
	No. samples											
Depth	16		8		16		16		8		16	
(m)	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
14-19	76	(94)	98	(78)	133	(159)	100	(59)	61	(68)	37	(47)
21-28	76	(122)	138	(101)	202	(207)	68	(76)	108	(89)	65	(62)
28-38	110	(95)	11	(79)	201	(161)	46	(59)	87	(69)	56	(48)
39-47	136	(87)	83	(72)	140	(148)	35	(55)	33	(63)	43	(44)
Total	398		330		676		249		289		201	
χ^2	52.19		78.89		14.73		39.46		23.77		3.63	

Total $\chi^2 = 212.69$ (15 df, $P < 0.005$)

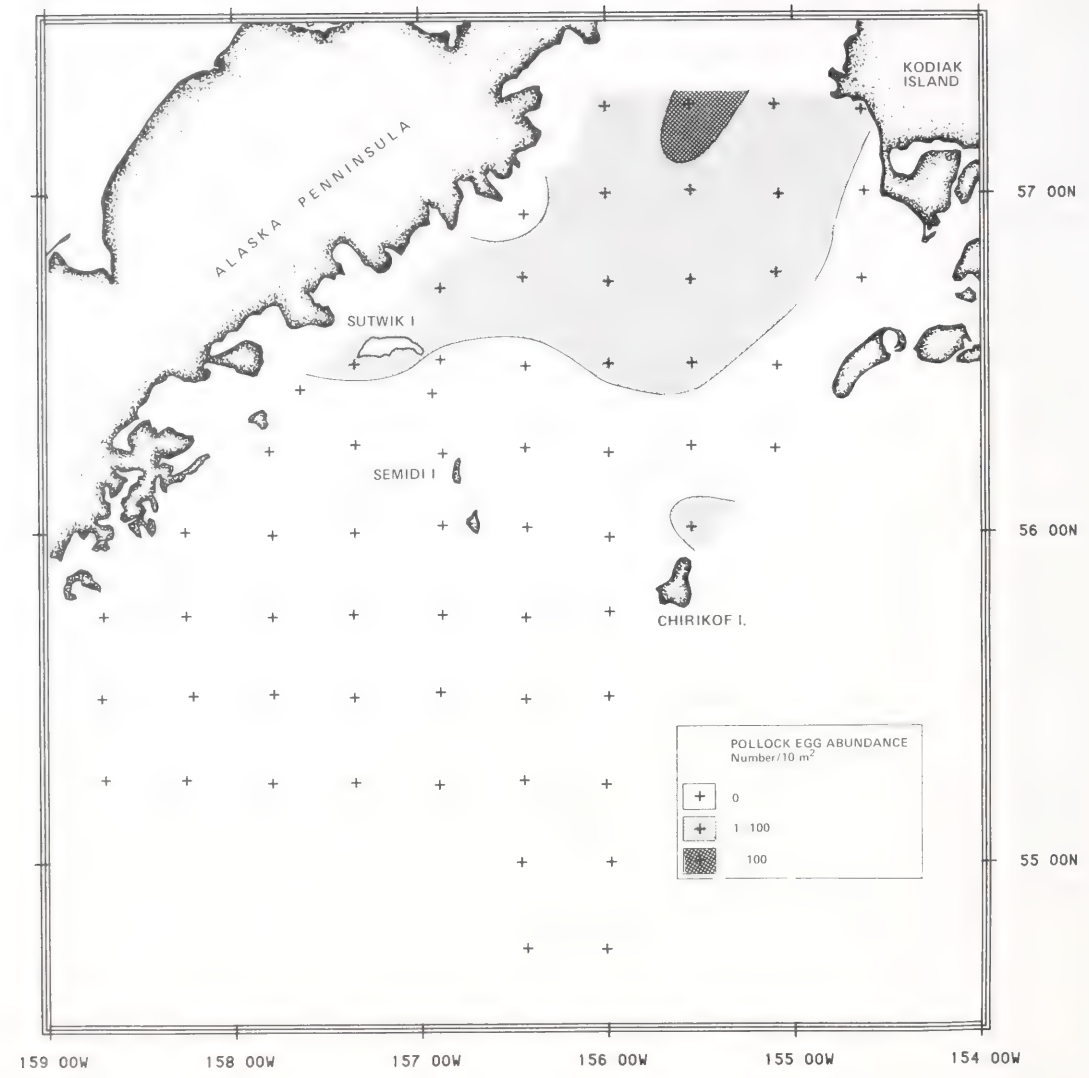

FIGURE 6.—Distribution and abundance of walleye pollock eggs, May 1983.

(Table 2). The means of the catch per 10 m^3 at each time-depth combination expressed as a percentage of the total catch at that time of day suggests a pattern of limited diel vertical migration (Fig. 7). The chi-square test was highly significant ($P < 0.005$) indicating that the null hypothesis, that the larvae were distributed at each depth in the same proportions among the different times, should be rejected. Examining the relative abundances within each time period, the larvae appeared to be concentrated above 20 m at 0630 h, and at 28-47 m by 1830 h (Fig. 7). They were most evenly distributed in the early afternoon and most abundant in the 21-28 m stratum during darkness (2230 and 0230 h) and at 1030 h. The lowest percent abundance at each time period shows a complementary pattern, with relatively small catches at 39-47 m from 0230-1430 h. This pattern was observed on both days during the 48-h sampling.

In summary, it appears that some larvae gradually move up in the water column from a depth of 30-50 m in the evening to above 20 m in early morning. They gradually descend during daytime, and are most evenly distributed in the early afternoon.

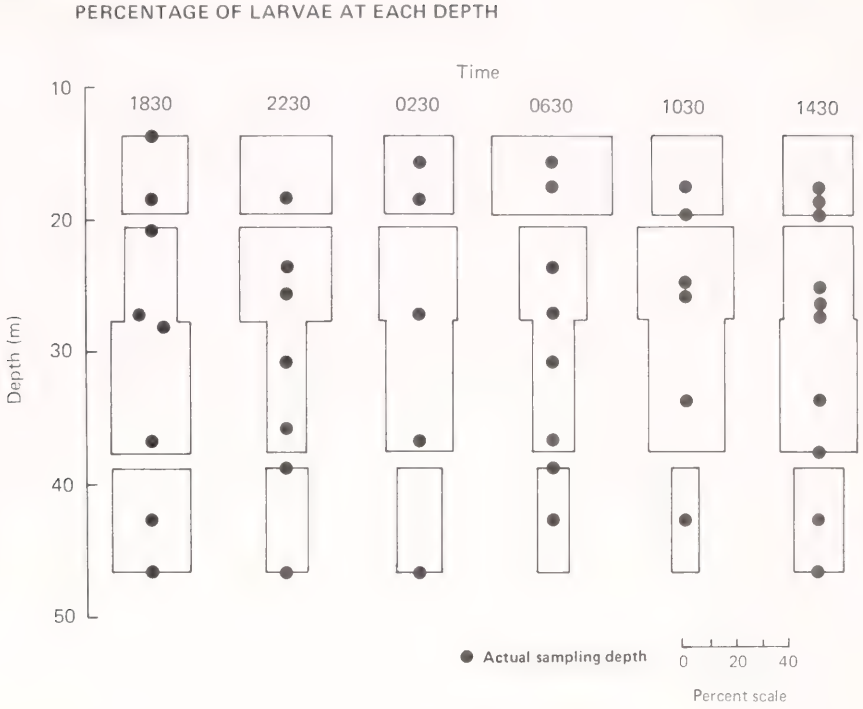

FIGURE 7.—Relative abundance as percent of larvae at each depth for each time interval, of walleye pollock larvae from the vertical distribution study, May 1983.

Comparison of Catches of Walleye Pollock Larvae by Different Gears

The sizes of larvae in the different bongo nets at the vertical distribution station were similar (Table 3). Mean lengths of larvae in the 20 cm bongo nets varied from 11.00 in the 333 μm mesh net to 11.10 mm in the 253 μm mesh net (SD = 1.76 and 1.69 mm respectively); mean length in the 60 cm bongo nets was 11.07 mm (SD = 1.77 mm). The Tucker trawl, however, caught larvae that had a mean length of 9.64 mm (SD = 1.67 mm). The overall mean abundance of larvae in the 20 cm bongo in the 28-38 m depth stratum nets (11.82 larvae/10 m^3) was similar to that in all the Tucker trawls (11.66 larvae/10 m^3) which were towed at 35 m. The mean of the catches in the 60 cm bongo nets, towed just below the deepest 20 cm bongo, was not notably different from the mean of those 20 cm bongo catches taken at the same times.

Variations in overall catches in the 20 cm bongo nets at the vertical distribution stations seemed to reflect the patchy nature of the concentration of larvae and not net avoidance related to time of day. The largest catches occurred during daylight, at 1030 h, while the smallest catches occurred during the time intervals immediately preceding (0630 h) and immediately following (1430 h) the largest catches. Since we sampled one geographic site rather than following a drogue, we probably sampled water with different concentrations of larvae as it drifted past us during the 48-h sampling. It appears that the larvae decreased from a concentration greater than 1 m^{-3} during the first 24 hours to <0.5 m^{-3} during the second 24 hours. The size of larvae did not change during the study again indicating that increased daytime net avoidance was not significant.

Hydrography in Relation to Distribution of Walleye Pollock Larvae

No obvious hydrographic features were associated with larval distributions. At the diel station, larvae were concentrated between 14 and 47 m where temperature within the upper 50 m was

TABLE 3.—Comparisons of catches and lengths (mm SL) of walleye pollock larvae with gear, time of day, and depth from the vertical distribution study, May 1983.

	mm SL (SD)	number	mm SL (SD)	number
	333 μm mesh		253 μm mesh	
Depth (m)				
14-19	11.13 (1.80)	333	10.86 (1.77)	333
21-28	11.07 (1.74)	405	11.07 (1.87)	427
28-38	11.24 (1.68)	232	11.04 (1.73)	290
39-47	11.19 (1.60)	249	11.17 (1.46)	229
Time (local)				
1830	11.03 (1.67)	210	10.86 (1.65)	118
2230	10.98 (1.58)	189	10.76 (1.56)	185
0230	11.50 (1.83)	315	11.39 (1.75)	361
0630	11.12 (1.42)	133	11.31 (1.82)	116
1030	11.01 (1.75)	331	10.61 (1.81)	301
1430	10.73 (1.57)	183	11.13 (1.72)	182
Gear				
20 cm bongos, 253 μm mesh	11.10 (1.69)	1,388		
20 cm bongos, 333 μm mesh	11.00 (1.76)	1,381		
All 60 cm bongos	11.07 (1.77)	578		
All Tucker trawls	9.64 (1.67)	2,180		

stable at 6.90°-6.15°C (Fig. 8). Nearby, salinity and density showed a very gradual increase with depth.

The pattern of water movement in the survey area, derived from the temperature and salinity observations, indicated a general southwest flow of water at all depths. In the area of larval concentration, most of the flow tended southward, following the deep trough from Shelikof Strait across the continental shelf between the Semidi Islands and Cherikof Islands (S. Kim[9]).

Diet and Feeding of Walleye Pollock Larvae

Eighteen different food items were identified in walleye pollock larvae sampled at the diel sta-

[9]S. Kim, School of Fisheries, University of Washington, Seattle, WA 98195, pers. commun. September 1985.

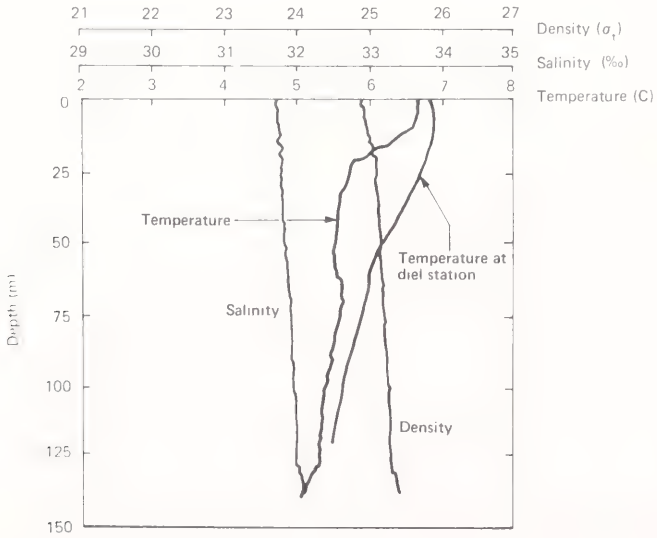

FIGURE 8.—Temperature, salinity, and sigma-t profiles at Station 47 with temperature profile from the diel station (Stations 63-77) shown for comparison. See Figure 2 for station locations.

tions. Copepod nauplii 90-600 μm in length and between 40 and 250 μm in width were the most abundant food item for larvae <14.0 mm (Fig. 9). The length- and width-frequency distributions of nauplii indicate that *Pseudocalanus* spp. and *Oithona* spp. are the likely prey taxa. Nauplii became numerically less important in diets of larger larvae. *Pseudocalanus* spp. copepodids, copepod eggs, and *Oithona* spp. copepodids made up a larger numerical portion of the food of these larger larvae (Fig. 10). The increased importance of *Pseudocalanus* spp. copepodids in the diet of larger larvae is evident in terms of gut volume (Fig. 10). Examination of the contribution of the copepod eggs to the diet indicates that while eggs increase numerically from 1.5% in the 8.0-8.9 mm size group to 55% in the 14.0-14.9 mm size group, their volume increases only from 0.5 to 3.6%.

The number of food organisms and mean prey volume per larva show a diel feeding pattern (Fig. 11). The maximum gut contents were observed during the afternoon. Collections at 2235, 0230, 0238, and 0629 have the lowest mean number of food items per larva, which suggests that feeding during darkness is reduced. The mean gut volumes show a similar pattern (Fig. 11). Although gut volume at 1047 h on 29 May was unusually low, it was not an indication of reduced feeding. Here the gut contents consisted of numerous copepod nauplii and few adult copepods. Thus the calculated prey volume is quite low, while the number of food items per gut is high.

Zooplankton Composition

Thirty-nine groups of zooplankters were identi-

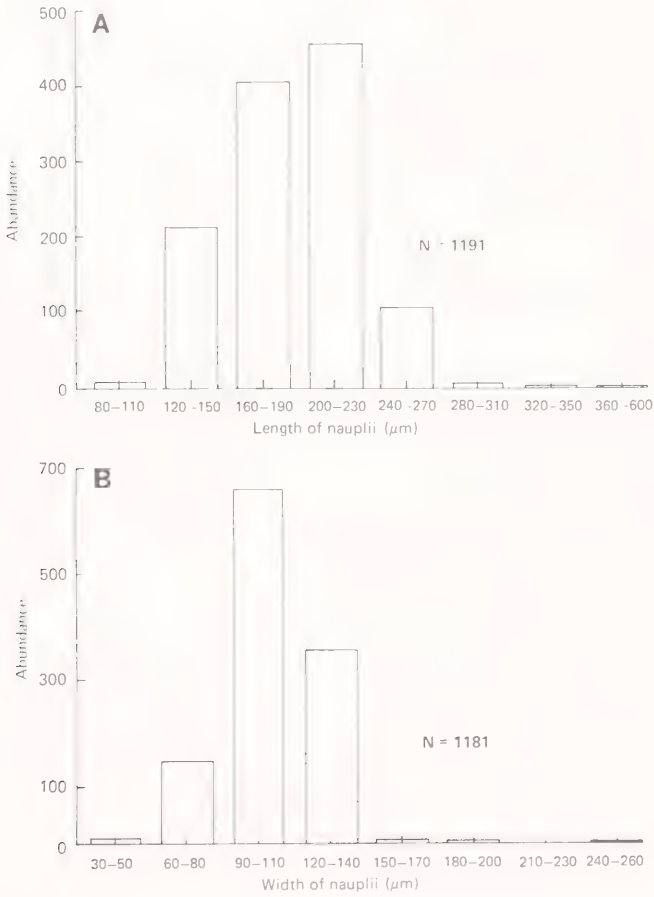

FIGURE 9.—Length (A) and width (B) size-frequency distribution of copepod nauplii from guts of walleye pollock larvae.

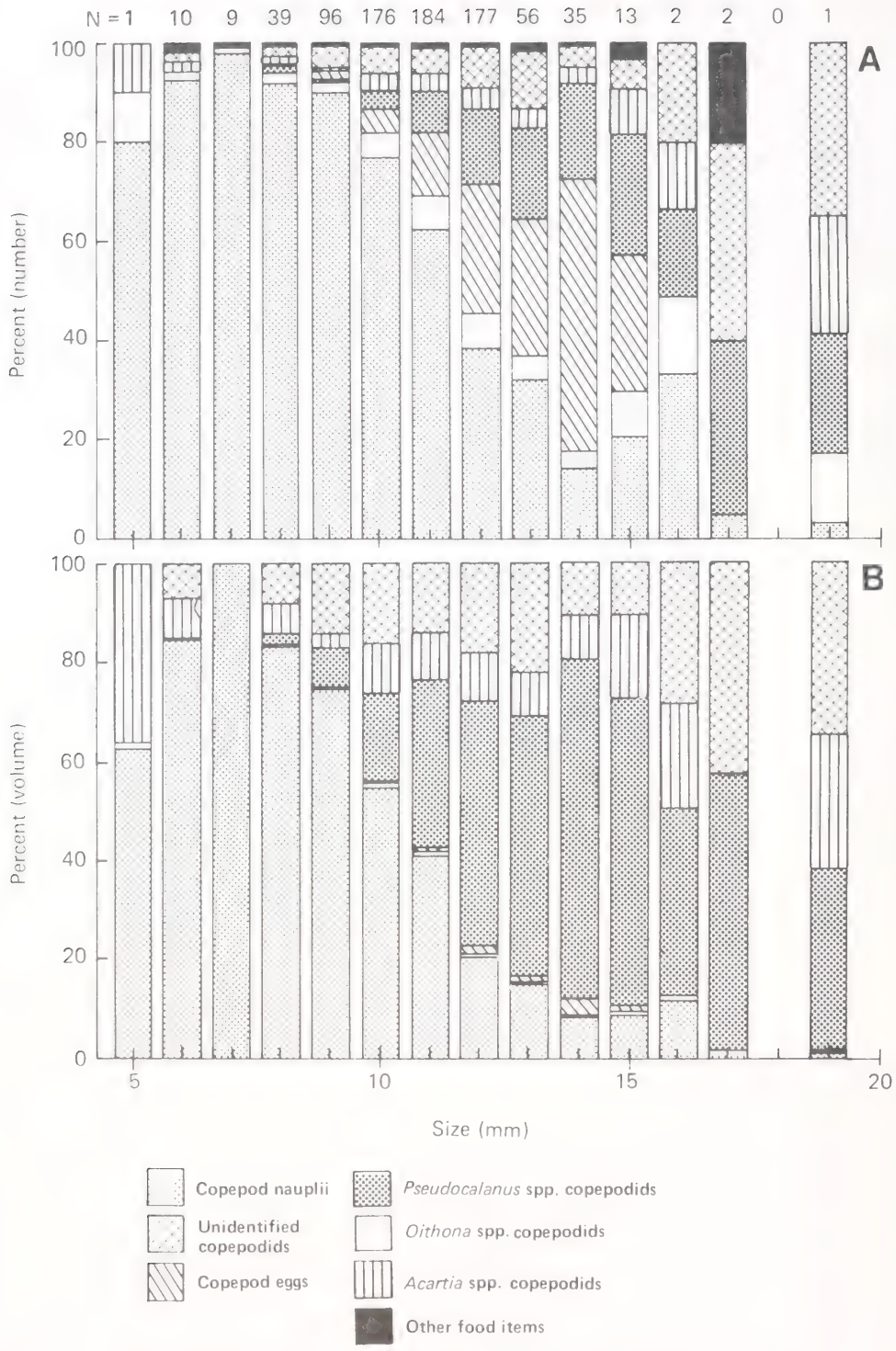

FIGURE 10.—Gut contents of walleye pollock larvae by 1 mm length intervals (5-20 mm) from northern Gulf of Alaska, May 1983. A—percent number; B—percent volume.

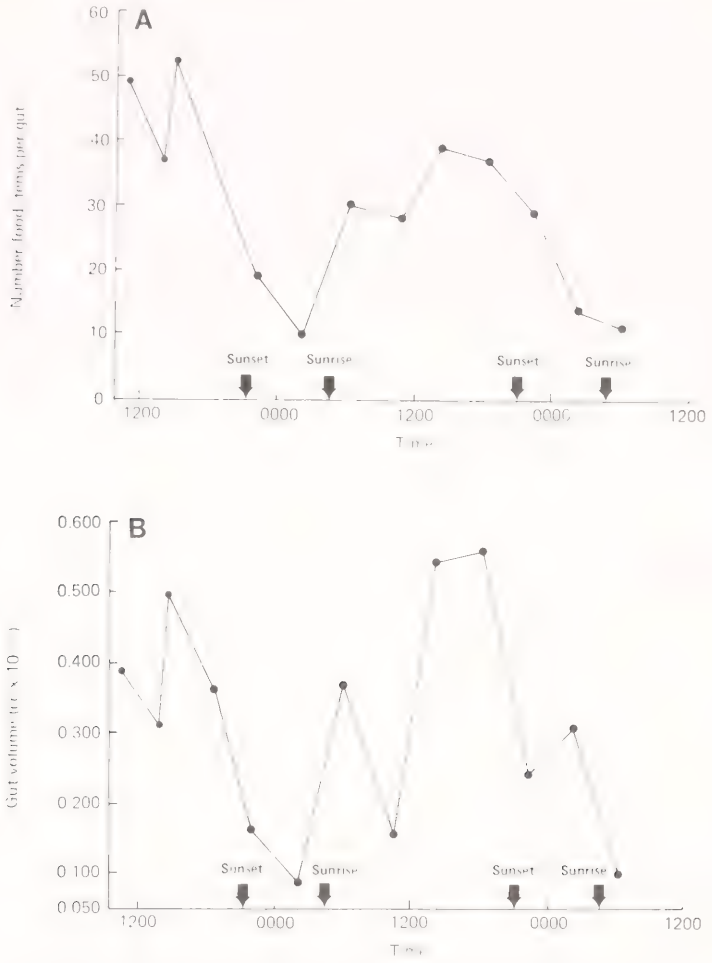

FIGURE 11.—Numbers of prey (A) and gut fullness (B) of walleye pollock larvae by time of day and depth from the vertical distribution stations, May 1983.

fied from samples taken with the 253 μm mesh net (Table 4). *Pseudocalanus* spp. were generally the most abundant taxon. Abundances of *Pseudocalanus* females ranged from 11 m^{-3} to a peak of 1,398 m^{-3} at 1515 h on the first day at a depth of 47 m. The overall mean abundance of *Pseudocalanus* females was 224 m^{-3}. These females comprised between 9 and 23% of the total zooplankton at all depth strata both during the daylight and darkness (Fig. 12). The highest percent contribution by this stage (22-23%) was during daylight hours at the two deepest strata. Peak abundances usually occurred at depth strata below 25 m. Copepodid stages of *Pseudocalanus* also reached a peak of 1,890 m^{-3} at the same station. These copepodids contributed the greatest percentage (21-33%) of the total zooplankton at all depths and times. There were no obvious patterns associated with depth or time of day in either abundance or percent composition of the total zooplankton.

Oithona spp. were abundant in the samples even though they were not collected quantitatively in the 253 μm mesh net. The peak abundance observed was 1,323 m^{-3}. *Oithona* spp. were most abundant in the surface stratum comprising 18% of the total zooplankton during the day versus <10% of the zooplankton at deeper strata during the day and at all depths during the night (Fig. 12). *Acartia* spp., *Neocalanus* spp., and *Calanus* spp. were the only other abundant copepods. The *Neocalanus* spp. and *Calanus* spp. in-

TABLE 4.—Species composition of zooplankton samples from the vertical distribution stations.

Number (See Fig. 11)	Taxon Name	Maximum No./10 m^3	Minimum No./10 m^3	Mean No. 10 m^3
1	*Pseudocalanus* spp. adult female	13,981	118	2,245
2	*Pseudocalanus* spp. adult male	4,711	0	567
3	*Pseudocalanus* spp. copepodids 1-5	18,915	46	3,592
4	*Neocalanus* spp. and *Calanus* spp.	12,163	0	1,545
5	*Oithona* spp.	13,234	0	1,167
6	*Acartia* spp.	2,476	101	794
7	*Centropages* spp.	380	0	50
8	*Metridia* spp.	—	0	—
9	*Eucalanus bungii*	192	0	7
10	*Paracalanus* sp.	46	0	5
11	*Clausocalanus* sp.	25	0	1
12	*Tortanus* spp.	7	0	—
13	Unidentified calanoid	201	0	9
14	Euphausiid furcilia	3,431	0	511
15	Euphausiid calyptopsis	97	0	7
16	Euphausiid crytopsis	—	0	—
17	*Thysanoessa inermis* furcilia	1,307	0	517
18	*T. inermis* calyptopsis	—	0	—
19	*T. inermis* crytopsis	97	0	5
20	Euphausiid juveniles	—	0	—
21	*T. inermis* juvenile	73	0	5
22	Chaetognatha	592	0	94
23	Appendicularia	1,088	0	290
24	Hyperidae	183	0	31
25	Gastropoda	484	0	62
26	Decapoda	262	0	24
27	Balanidae	253	0	39
28	Gammaridae	7	0	—
29	*Evadne* spp.	97	0	3
30	*Limacina* spp.	1,569	0	364
31	Pontellidae	19	0	—
32	Thecosomata	255	0	21
33	Brachyura	292	0	34
34	Gymnocomata	38	0	1
35	Echinodermata	1,511	0	117
36	Hydrozoa	311	0	18
37	Pelecypoda	28	0	1
38	Medusa	14	0	—
39	Siphonophore	8	0	—

cluded *N. plumchrus*, *C. pacificus*, and *C. marshallae*. Together these species contributed between 13 and 25% of the total zooplankton (Fig. 12).

Euphausiids were the only other abundant group of zooplankters; furcillae were the most abundant stage. The abundance of furcillae was generally <200 m^{-3}; however, at 1047 h on 29 May, the numbers of furcillae exceeded 1,300 m^{-3}.

Age and Growth

Ages were determined for 109 walleye pollock larvae, including 40 individuals collected from Station 37 within the area of highest larval abundance and 69 specimens from four stations well removed from this area. Standard lengths ranged from 6.0 to 14.6 mm and mean increment counts (days since hatching) ranged from 7 to 45.5 (Table 5). The average growth rate varied from 0.12 to 0.25 mm/day among the five stations (Table 5). When compared pairwise with growth rates from all other stations, growth rates from all stations located outside the dense patch, ex-

TABLE 5.—Average growth rates, statistics on the linear regression, comparison lengths, and ages of larval walleye pollock used in growth analysis from five areas in the Shelikof Strait. Station 37 is in the area of highest larval density (Fig. 1).

Station	*Y*-intercept (mm)	*b*-growth (mm d^{-1})	r^2	*N*	No. of fish aged	Length range (mm)	Age range (days)
37	3.7	0.24	0.82	40	40	6.8-13.1	12-42
53	4.2	0.23	0.81	20	20	7.6-13.0	20-41
9	3.5	0.25	0.81	20	20	6.0-14.6	7-43
6	4.7	0.18	0.61	20	20	6.6-12.3	10.6-42.2
12	6.6	0.12	0.90	9	9	8.1-12.6	14-45.5

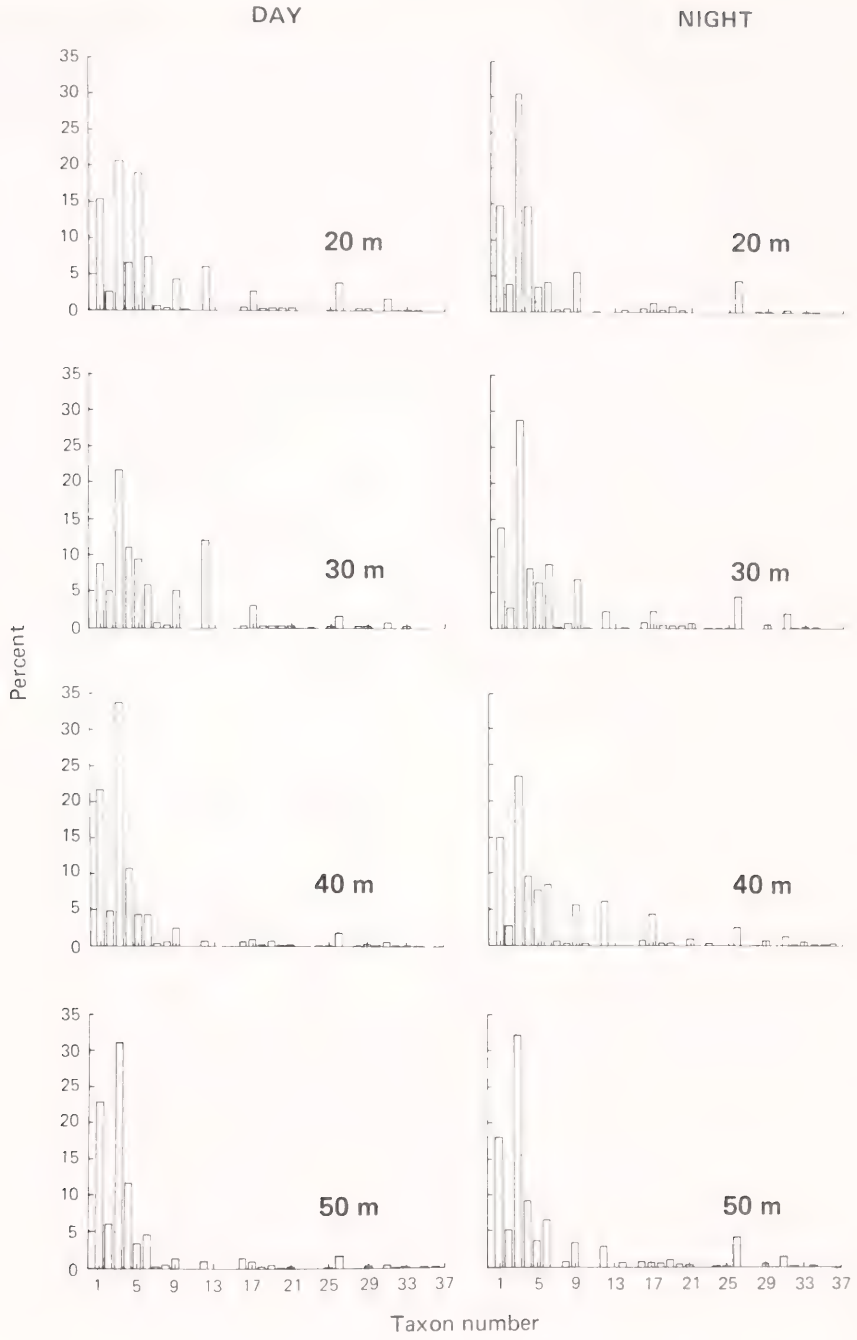

FIGURE 12.—Zooplankton distribution (percent total zooplankton) for day and night by depth from the vertical distribution stations, May 1983. Taxon numbers: 1: *Pseudocalanus* spp., adult female; 2: *Pseudocalanus* spp., adult male; 3: *Pseudocalanus* spp., copepodids 1-5; 4: *Neocalanus* spp. and *Calanus* spp.; 5: *Oithona* spp.; 6: *Acartia* spp.; 7: *Centropages* spp.; 8: *Metridia* spp.; 9: *Eucalanus bungii;* 10: *Paracalanus* sp.; 11: *Clausocalanus* sp.; 12: *Tortanus* spp.; 13: Unidentified calanoid; 14: Euphausiid furcilia; 15: Euphausiid calyptopsis; 16: Euphausiid crytopsis; 17: *Thysanoessa inermis* furcilia; 18: *T. inermis* calyptopsis; 19: *T. inermis* crytopsis; 20: Euphausiid juveniles; 21: *T. inermis* juvenile; 22: Chaetognatha; 23: Appendicularia; 24: Hyperidae; 25: Gastropoda; 26: Decapoda; 27: Balanidae; 28: Gammaridae; 29: *Evadne* spp.; 30: *Limacina* spp.; 31: Pontellidae; 32: Thecosomata; 33: Brachyura; 34: Gymnosomata; 35: Echinodermata; 36: Hydrozoa; and 37: Pelecypoda.

cept Station 12, were not statistically different from growth measured within the dense patch (Station 37). Larvae collected at adjacent Stations 6 and 12, located to the northeast of the densest area (Fig. 2), exhibited the lowest growth rates and were not statistically different from each other.

Estimated age-at-length data from all stations were combined to describe early growth in walleye pollock from the Shelikof Strait region as follows:

$$SL = 4.29 + 0.21 \text{ (age, d)} \qquad n = 109,\ r^2 = 0.75$$

where SL = standard length (Fig. 13). This relationship suggests a mean growth rate of 0.21 mm/day and an intercept of 4.29 mm, which corresponds with the known size of newly hatched larvae (Walline 1983; Nishimura and Yamada 1984).

The distribution of dates of hatching was estimated by back-calculating from the ages determined for larval walleye pollock in the Shelikof Strait. The median birthdates from all stations were similar and thus all 109 samples were combined (Fig. 14). The hatching period ranged from early April to mid-May with a mode in the last

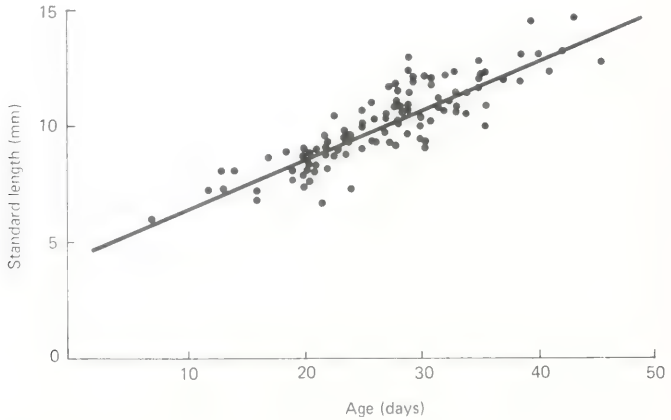

FIGURE 13.—Estimated age at length, fitted with linear regression, for all walleye pollock larvae analyzed from the northern Gulf of Alaska, May 1983.

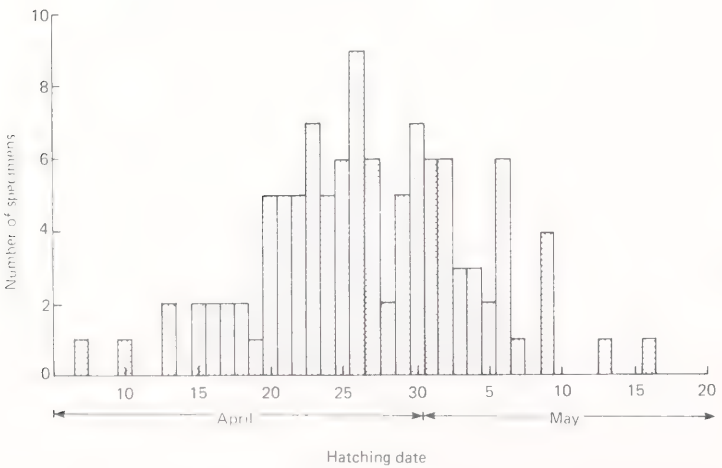

FIGURE 14.—Distribution of hatching dates for walleye pollock determined by back-calculation using age and date of collection.

week of April. Incubation time for walleye pollock eggs held at 5°-6°C in the laboratory is estimated to be 14 days (Haynes and Ignell 1983; Nakatani and Maeda 1984; Nishimura and Yamada 1984); spawning of walleye pollock occurs primarily in late March and early April in Shelikof Strait (Dunn et al. fn. 5), supporting our estimated hatching dates distribution.

DISCUSSION

Relative Abundance of Eggs and Larvae

Neuston collections in spring in the northern Gulf of Alaska have been reported only for 1978, mainly over the shelf, south and east of Kodiak Island, a month earlier than the present study (Kendall and Dunn 1985). Eggs of *Theragra chalcogramma* were most abundant; the rest of the identified eggs were of several pleuronectids. The greater abundance of *T. chalcogramma* in relation to the pleuronectids in the earlier cruise, when compared with the present data (Fig. 5), probably reflects the seasonal difference in spawning times. Pleuronectids spawn mainly in late spring and early summer in the Gulf of Alaska while *T. chalcogramma* is mainly a late winter-early spring spawner (Kendall and Dunn 1985).

Eggs have been reported from bongo catches from three other cruises in the northern Gulf of Alaska in May (Bates and Clark 1983[10]; Kendall and Dunn 1985); eggs of pleuronectids and those of *T. chalcogramma* were most abundant. However, the rank order of abundance of the various pleuronectids varied considerably among the cruises. Usually eggs of *Glyptocephalus zachirus*, *Hippoglossoides elassodon*, and *Microstomus pacificus* were among the five most abundant taxa.

Among larvae in the neuston tows during the present study, mainly spring spawning taxa (e.g., *Ammodytes hexapterus*, *Bathymaster* spp., *T. chalcogramma*) were represented; whereas larvae of fall-winter spawning taxa (e.g., three hexagrammids, and *Hemilepidotus* spp. [Irish lords]) were abundant during the earlier cruise (Kendall and Dunn 1985).

In bongo catches during other May cruises in the area, larvae of *T. chalcogramma*, *Hippoglossoides elassodon*, *Bathymaster* spp., and *A. hexapterus* have always occurred frequently, as in the present study (Bates and Clark fn. 9; Kendall and Dunn 1985).

Distribution of Walleye Pollock Eggs

The few eggs collected during the present study represented a very late part of the spawning, which occurs in Shelikof Strait mainly in early April (Dunn et al. fn. 5) (Fig. 1). Recently hatched larvae (<5 mm SL), which were collected during our survey (Fig. 2), also indicate prolonged spawning but probably at a low level after mid-April. The eggs we found were mainly over the deep waters at the southwest end of Shelikof Strait, and it would be expected that they were also farther to the northeast. This is the same area of occurrence of eggs during the height of spawning (Dunn et al. fn. 5), indicating that the adults spawn mainly in Shelikof Strait throughout this period, although individual spawning fish probably migrate in and out of the area.

Comparisons of Distribution of Walleye Pollock Larvae

In 1981, several sequential cruises to Shelikof Strait mapped a large concentration of walleye pollock eggs in early April; and in late April and again in mid-May, a concentration of larvae was found progressively further to the southwest of the area where the eggs had been (Bates and Clark fn. 10) (Fig. 1). The size of the larvae in the concentration increased between the cruises.

Sampling in 1981 and 1982 for walleye pollock larvae was at the same area and time (24-28 May) as the present study (Dunn et. al. fn. 5). Comparisons of distribution, abundance, and size of the larvae among these 3 years reveal remarkable differences (Table 6). Spawning time in 1981, based on ages of eggs caught in early April, and presence of newly hatched larvae in late April, centered around 5-8 April. In 1983, based on birthdate distributions presented here, modal spawning time was also in the second week of April. Sampling in subsequent years has shown a remarkable consistency in spawning place and time (Kendall unpubl. data). By 24-28 May the patch of larvae in 1981 and 1983 had drifted to the same area, just north of Sutwik Island (Figs.

[10]Bates, R. D., and J. Clark. 1983. Ichthyoplankton off Kodiak Island and the Alaska Peninsula during spring 1981. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 83-09, 105 p.

TABLE 6.—Concentrations and lengths of pollock larvae collected 24-28 May 1981, 1982, and 1983 in the patch resulting from the Shelikof Strait spawning (1981 and 1982 data from Dunn et al. text fn. 5).

Year	Cruise	Date (May)	Stations	Larvae m^{-2}	Lengths (mm SL) Mean	SD
1981	4MF81	24	73, 74	2,318	7.36	1.11
	3SH81	25	225	1,285 (mean = 2,040)	7.77	1.18
1982	2DA82	24-28	108, 115, 117, 123, 124, 126	14-38 (mean = 23)	7.74	1.10
1983	1CH83	24, 28	31, 32, 36, 37, 63	104-214 (mean = 151)	11.23	1.65

1, 2). However, the abundance of larvae in 1981 was about 2,000 m^{-2} while in 1983 it was only about 150 m^{-2}. Mean length in 1981 was about 7.5 mm while in 1983 it was 11.2 mm. Since the spawning dates were the same, this would indicate a much slower growth rate (about 0.09 mm d^{-1}) in 1981 than in 1983 (0.21 mm d^{-1}). In 1982 there were fewer larvae (20 m^{-2}) and they were distributed further southwest than in the other 2 years (Dunn et al. fn. 5). These larvae were not different in length from those in 1981 (7.7 mm). The position of the larvae in 1982 suggests a much faster drift than in 1981 and 1983.

Although most of the spawning occurs in the deep trench (>200 m) in Shelikof Strait, the larvae are in the upper part of the water column. Southwest of Shelikof Strait the trench runs south between the Semidi Islands and Chirikof Island (Fig. 2). Early larvae drift in the Alaska Coastal Current which flows southwest, parallel to the Alaska Peninsula (Schumacher and Reed 1980). At the time of our surveys in May 1981 and 1983, larvae had drifted to the area between Sutwik Island and the Semidi Islands. In 1982 they were further to the southwest in water over the deeper trough and the continental shelf.

Vertical Distribution of Walleye Pollock Larvae

Vertical distribution of walleye pollock larvae has been addressed in detail in several other studies (Kamba 1977; Cooney et al. 1978; Walline 1981[11]; Dagg et al. 1984). Although the areas of study, procedures, and gear have varied, a consistent pattern of diel-vertical distribution emerges from these studies and is supported by the present study. Haryu (1980) summarized his and earlier work by stating "larvae inhabit the mid-layer rather than the surface layer and perform diurnal vertical migration in search of food." Most larvae have been found between 10 and 60 m, and within this depth range, some larvae generally move to shallower depths at night. Vertical movement is not pronounced in any of the studies but is evident by comparing proportions of larvae at various sampling depths at different times of day. In general it appears that larvae <15 mm are most concentrated vertically at 10-15 m at twilight, both in the evening and morning. During nighttime and daytime the larvae are more dispersed vertically, and during daytime their distribution is deeper than at night. Samples confined to day and night periods do not show the crepuscular nature of the distribution. This pattern is seen in the present study but is less pronounced than in some others, possibly because we conducted our sampling only in the vertical range of high concentration. Larvae larger than about 15 mm appear able to avoid plankton nets to some extent, particularly during daytime. The available data, however, suggest that these larger larvae remain concentrated in a shallow depth stratum (5-15 m) except at night when they are more dispersed vertically and may rise closer to the surface (Walline fn. 11).

Fish larvae of most other species that have been studied also migrate upward in the water column at night (Kendall and Naplin 1981). Some species undergo a much more pronounced vertical migration than is apparent with walleye pollock larvae and may cross much greater temperature gradients than observed here. Similar to walleye pollock, larvae of other fish species are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Walleye pollock larvae may move to shallower depths at night to allow more feeding in reduced light. They then may spread downward in the water column during daytime in response to increased light penetration and the distribution of their prey. Too little is known about predation on fish larvae to assess the importance of vertical movements on predator avoidance (see Incze et al. 1984).

[11]Walline, P. D. 1981. Hatching dates of walleye pollock (*Theragra chalcogramma*) and vertical distribution of ichthyoplankton from the eastern Bering Sea, June-July 1979. U.S. Dep. Commer., Natl. Mar. Fish. Serv., NOAA, NWAFC Proc. Rep. 81-05, 12 p.

Feeding of Walleye Pollock Larvae

The diet composition of larval walleye pollock in Shelikof Strait is similar to that described for walleye pollock larvae collected in the southeastern Bering Sea (Clarke 1978) and Uchiura Bay, Hokkaido, Japan (Kamba 1977). Copepod nauplii and copepodids of *Pseudocalanus* spp. were the dominant food items in the guts of 6-20 mm larvae in all these studies. As in this study, copepod eggs were also abundant food items. It is difficult in any of these studies to judge if the eggs were captured as individual food items or along with adult female copepods.

Feeding by larvae in the Gulf of Alaska is highest during daylight hours, as observed in other studies (Kamba 1977; Clarke 1978). Clarke (1978) reported that the few collections made at sunrise had larvae with the lowest feeding incidences. Kamba (1977) also reported that the lowest feeding incidences and the lowest abundance of food in the gut occurred near sunrise.

The high densities of larvae in the Shelikof Strait seem to have little effect on their food habits. *Oithona* spp. are abundant in the Bering Sea, Gulf of Alaska, and Uchiura Bay, Japan, and are intermediate in size between *Pseudocalanus* spp. copepodids and copepod nauplii. *Oithona* are an important component of the diet of pollock larvae in the Bering Sea, accounting for more than 25% of the total number of food items for larvae between 11.8 and 17.7 mm (Clarke 1978), but are rare in guts of larvae collected near Hokkaido (Kamba 1977), and represent <16% of the food items for all size groups in the present study. Kamba (1977) cited the low incidence of occurrence of this food item in larvae collected in Uchiura Bay as evidence of selective feeding by walleye pollock larvae.

The zooplankton species composition in the oceanic and outer shelf regions of the Bering Sea (Cooney and Coyle 1981; Smith and Vidal 1984) is similar to that described for the northern Gulf of Alaska and Ocean Station P (Le Brasseur 1965; Damkaer 1977; Fulton 1983; Miller et al. 1984). The Shelikof Strait species composition is similar to these areas. Our zooplankton sampling did not include copepod nauplii so we cannot assess their abundance. The size distribution of copepod nauplii ingested, however, indicates that *Pseudocalanus* spp. and *Oithona* spp. are the probable sources of the copepod nauplii ingested by larval walleye pollock in Shelikof Strait.

Daily production of copepod nauplii at a single station in the Bering Sea has been estimated to be 27,094 m^{-2}, of which more than 95% was *Pseudocalanus* spp. (Dagg et al. 1984). The abundance of *Pseudocalanus* females ranged from 9.9 to 258.9 m^{-3} ($\bar{x}$ = 87.7). The mean abundance of *Pseudocalanus* females in Shelikof Strait was 244 m^{-3}, or 2.6 times greater than the mean abundance in the Bering Sea. Assuming the same rate of daily production, about 69,000 nauplii m^{-2} would be produced in Shelikof Strait. Mean abundance of walleye pollock larvae where Dagg et al. (1984) performed their study was 6.3 larvae m^{-2}, whereas at the diel station in Shelikof Strait the abundance was 156 m^{-2}, about 25 times greater than in the Bering Sea study. If these larvae ate nauplii at the same rate as those in the Bering Sea, 18.3 per day, they would eat about 24% of the production, as opposed to the <1% in the Bering Sea. Other factors such as the relationship between size of larvae and daily ration need to be investigated before more precise estimates of the impact of larval feeding and the possibility of food limitation can be made. It appears that enough nauplii were being produced to preclude density dependent food restrictions at the larval densities observed in the present study.

Growth of Walleye Pollock Larvae

Growth rates were similar in areas of both high and low density (Table 5, Fig. 13). It cannot be determined from our study whether density-dependent factors modified larval growth; growth variations could be produced by patchy distributions of prey. Walleye pollock larvae have been shown to grow faster in the laboratory at higher food densities (Bailey and Stehr 1986), further, where lower or constant larval densities interact with variable prey density, field studies have shown variability in growth (Govoni et al. 1985). Without knowledge of prey availability at each location, however, it is difficult to discern if high densities of prey coincide with dense patches of larvae. The relatively low growth rates found at two adjacent stations outside the patch (Stations 6, 12; Table 6) might indicate an area of less than adequate prey availability.

Growth rates for fishes can be influenced by environmental factors such as temperature, as well as availability of adequate food supplies (Boehlert and Yoklavich 1983). Within species,

growth rates are usually positively correlated with temperature over the normal temperature range. Growth rate for larval walleye pollock in the Gulf of Alaska (0.21 mm d^{-1}) is considerably lower than that determined for larvae of the same size range (4-25 mm SL) collected in the southeastern Bering Sea in June-July 1979 (0.35 mm d^{-1}, Walline 1985). Water temperatures were similar in both studies (about 6°-8°C). Maximum growth determined for larvae collected in the Bering Sea in March-June 1980 while water temperature was much cooler (2°-6°C), was 0.22 mm d^{-1} (Clarke 1984). Thus differences in growth rates of larval walleye pollock in the Bering Sea could be due to differences in water temperature, food availability, or a variety of other factors which may affect growth in larvae (Bailey and Stehr 1986). Future research on growth variability in the field should take into account prey availability, temperature, and size-specific mortality rates.

SUMMARY

1. Walleye pollock in the Gulf of Alaska form an intense spawning aggregation in Shelikof Strait in late winter that produces a dense patch of planktonic eggs in early April. Larvae from this spawning can be followed as they develop and are carried by currents to the southwest during spring.
2. In late May 1981, the density of larvae in this patch (>10 m^{-3}) suggested that density-dependent effects on growth and survival might be expected. A field study of larvae in late May 1983 found maximum densities of only 1 larva m^{-3}, and investigated growth and vertical distribution, and feeding in the patch.
3. The larvae were concentrated vertically between about 15 and 50 m, and tended to be in the upper part of this range during night and early morning, whereas they were deeper during the afternoon and evening.
4. Larvae <10 mm fed primarily on copepod nauplii, with copepodids becoming more important in larvae up to 20 mm. Copepodids of *Pseudocalanus* spp. made up a large fraction of the diet of larvae >10 mm. Most feeding occurred during daylight.
5. The copepods *Pseudocalanus* spp., *Neocalanus* spp., *Calanus* spp., *Oithona* spp., and *Acartia* spp. dominated the net zooplankton samples (253 μm mesh net).
6. Growth, based on otolith increments counted on 109 larvae (6.0-14.6 mm) was linear (0.21 mm/day, intercept = 4.29 mm, $r^2 = 0.75$). Growth rates in the area of high abundance were generally not significantly different from those elsewhere.
7. While at the larval densities observed in 1981, density-dependent effects are possible, at the lower densities we observed in 1983 no such effects were expected or indicated in growth rates or diet. Future studies should include direct measurement of copepod naupliar production rates in the areas inhabited by the larvae.

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ASPECTS OF THE BIOLOGY OF THE HAIR CRAB, *ERIMACRUS ISENBECKII*, IN THE EASTERN BERING SEA

THERESE M. ARMETTA[1] AND BRADLEY G. STEVENS[2]

ABSTRACT

The distribution and relative abundance of the hair crab, *Erimacrus isenbeckii*, were determined from data collected during annual summer trawl surveys conducted by the National Marine Fisheries Service (NMFS) in the eastern Bering Sea, 1979-84. The estimated population was about 23 million crabs from 1979 to 1981, but declined sharply to 4.4 million by 1984. The majority (67%) of the population occurred in the Pribilof Islands area. Male crabs occurred at a mean temperature of 3.4°C and depth of 66 m, whereas females occurred at a mean of 2.4°C and 64 m. Females comprised <10% of the catch in NMFS surveys. Over 99% of the females caught were mature, but only eight were ovigerous with from 34,000 to 160,400 eggs. Length-width and length-weight relationships were calculated for males and females. The majority (77%) of *E. isenbeckii* caught during an independently conducted study in May 1983 were found on a mixed sand and shell substrate. Scientific literature (mostly Japanese) was reviewed to provide information on larvae, reproduction, molting, growth, feeding habits, predation, migration, behavior, fishing, and marketing.

The hair crab, *Erimacrus isenbeckii* (Brandt) (Fig. 1), is a medium-sized brachyuran in the family Atelecyclidae. Hair crab have been fished in Japanese and Korean waters for over 60 years (Kawakami 1934), and much literature is available on the biology, distribution, and abundance of the species in those waters. In contrast, fishing for hair crab in U.S. waters began in 1979 (Griffin and Dunaway 1985[3]). The recent development of a U.S. fishery for hair crab and the substantial decline of the eastern Bering Sea (EBS) population from 1981 to 1984 prompted an analysis of hair crab data collected by the National Marine Fisheries Service (NMFS) during the summers of 1979-84. This report presents data on the distribution and abundance of hair crab in the EBS during those years, as well as aspects of ecology, reproduction, molting, and growth. Additionally, we have summarized the literature concerning this species, since most of it is published in Japanese and not easily accessible to English-speaking readers.

REVIEW OF PUBLISHED LITERATURE ON *ERIMACRUS ISENBECKII*

The hair crab has a quadrangular carapace slightly longer than it is wide, and is densely covered with short bristles and sharp granular projections; seven teeth are present on each lateral margin. Chelipeds and walking legs are stout and spiny. The epistome has a nearly straight anterior margin. Rathbun (1930), Sakai (1939), and Kobyakova (1955) described the morphology of adult *E. isenbeckii* in detail. Five zoeal stages and one megalopa stage in the development of this crab are described by Kurata (1963). According to Kurata, the zoeae are relatively large, ranging from 2.7 to 6.5 mm in body length (orbit to midpoint of posterior edge of telson), depending on zoeal stage, and are equipped with a long dorsal spine (1.2-2.8 mm) and prominent lateral spines that are about one-fourth of the length of the dorsal spine. Abdominal margins of the carapace are fringed with setae; abdominal segments possess knobs, spines, and spinules. The megalopa is about 7.2 mm long. The rostrum is short and wide and ends anteriorly in three short teeth. Abdominal segments lack spines.

In the EBS, hair crab occur from the northern

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[3]Griffin, K., and D. Dunaway. 1985. Bering Sea area shellfish management report to Alaska Board of Fisheries. *In* Westward region shellfish report to the Alaska Board of Fisheries, p. 179-245. Alaska Department of Fish and Game, P.O. Box 308, Dutch Harbor, AK 99692.

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FIGURE 1.—Male hair crab, *Erimacrus isenbeckii*, from eastern Bering Sea. Dorsal view.

shore of the Alaska Peninsula to the Pribilof Islands and St. Matthew Island (Fig. 2). Hair crab are also found along the Aleutian Archipelago from Unimak Island as far west as long. 170°E (west of Attu Island; NMFS unpubl. data). In the western Pacific, hair crab occur along the eastern coast of Korea, the western and eastern coasts of Japan, and southern Sakhalin Island (Rathbun 1930; Tanikawa 1971). They are particularly abundant around the island of Hokkaido and along the Kurile Islands to southern Kamchatka, and are common along west Kamchatka to lat. 54°40′N (Vinogradov 1947). They are unknown from the western Bering Sea.

Dall reported hair crab from Kachemak Bay and Cook Inlet, AK (Rathbun 1930). These, however, were probably *Telmessus cheiragonus*, a similar atelecyclid that commonly occurs in the northern Gulf of Alaska (Calkins 1978), since no verified observations of hair crab have been reported east of Unimak Island despite numerous inquiries to commercial fishermen and biologists working in the northern gulf in recent years.

Sakurai et al. (1972) (Fig. 3, bottom) reported that primiparous (first time breeders) female hair crab off Hokkaido mate from December to February and multiparous (have bred more than once) females mate from August to November (the latter in deeper waters than the former). According to Sakurai et al., mating occurs immediately after molting when females are in the soft-shell condition. When the female is ready to molt, a male crab grasps her chelipeds and holds on to them until after ecdysis. While the female is still soft, the male inserts his copulatory processes into her genital openings and fills the spermathecae with seminal fluid containing spermatophores. The male then secretes a mucoid, proteinaceous substance from his seminal glands which congeals immediately into hard plugs that firmly close the female's genital apertures. The male may then mate with other receptive females. Primiparous

FIGURE 3.—Average molting (top, Abe 1984, see text footnote 13) and breeding (bottom, adapted from Sakurai et al. 1972) cycles of *Erimacrus isenbeckii* (through age 8) offshore of southeastern Hokkaido. It is uncertain when eggs hatch after the second spawning period. Carapace lengths were measured from the notch between the rostral spines. "C" numbers indicate postlarval instars.

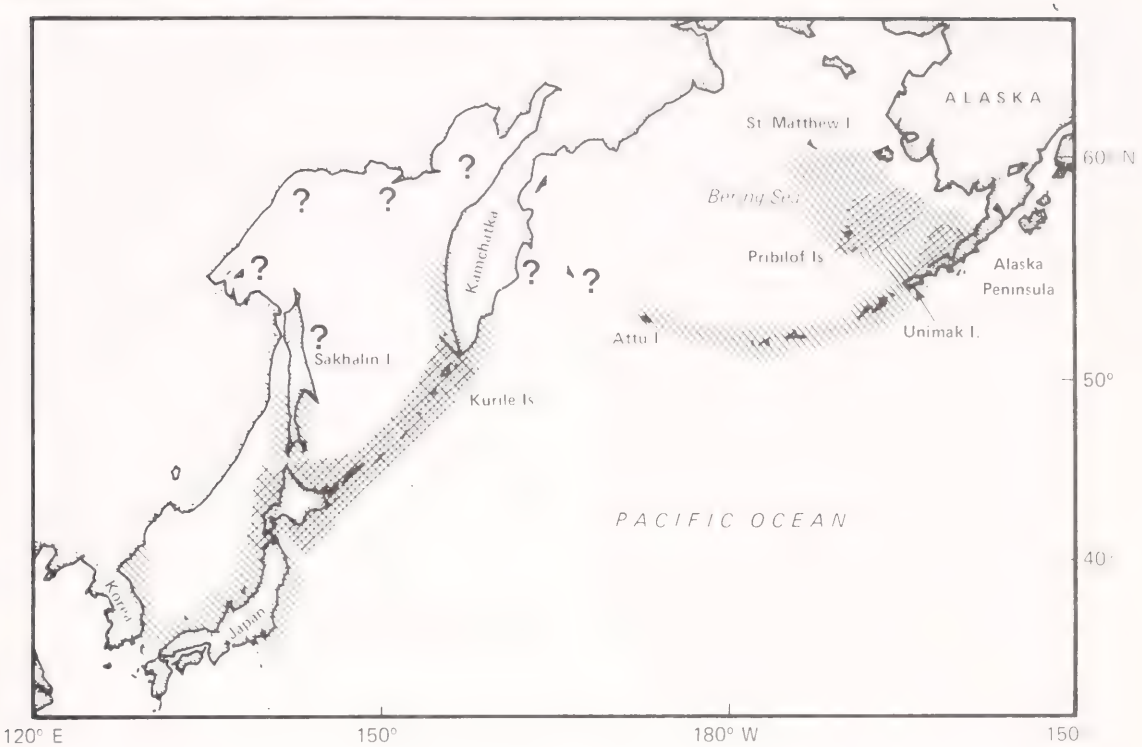
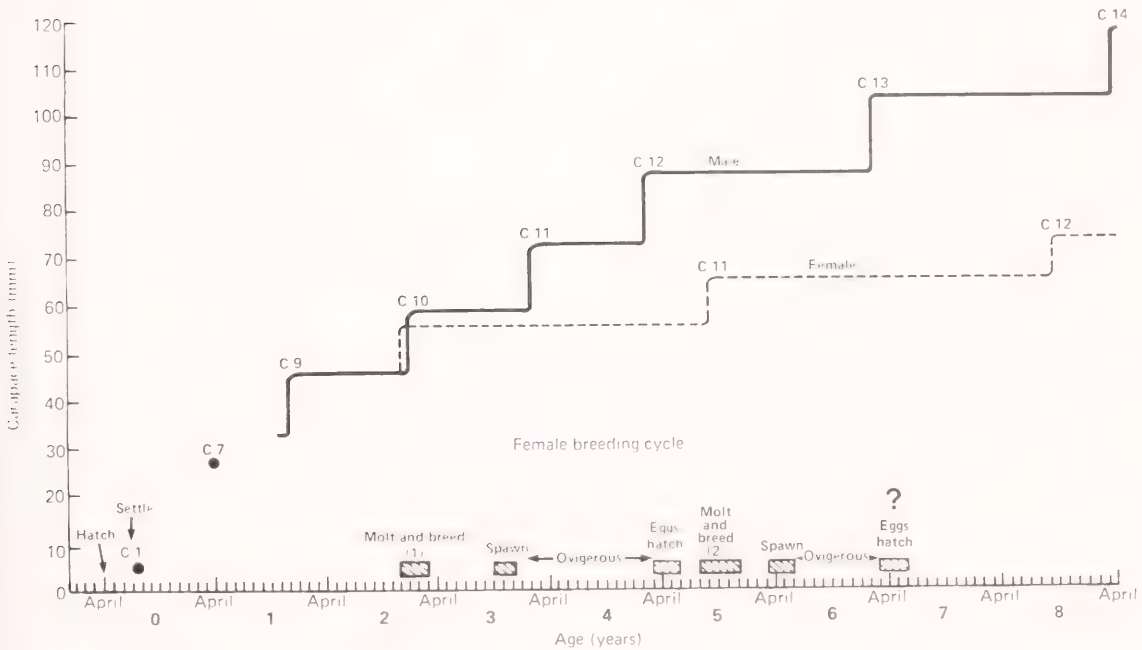


FIGURE 2.—Known world distribution of *Erimacrus isenbeckii*. Areas of high and low density are indicated by crosshatching and parallel lines, respectively. Question marks indicate areas where hair crab are believed to occur but are not well documented.



females extrude eggs in October and November while multiparous females extrude eggs from March to May (Fig. 3) (Sakurai et al. 1972). This indicates a 4-10 mo interval between copulation and extrusion. Yoshida (1940) suggested that spawning occurs only in alternate years.

Oocytes are yellowish white and immature at the time of copulation in both primiparous and multiparous females. During the interval between copulation and extrusion, the oocytes mature into dark orange ova 0.6 mm in diameter (Sakurai et al. 1972). After extrusion, the embryos are carried for at least a year during which time they become dark brown; hatching occurs from about March to May. Sakurai et al. reported that an average of 40,000-50,000 eggs and a maximum of 160,000 eggs were produced and that external embryos were 0.8-0.9 mm in diameter.

The distribution and timing of the occurrence of hair crab larvae near Hokkaido, the Kamchatka Peninsula, and in the eastern Bering Sea have been the focus of several studies. Near Hokkaido, Takeuchi (1969) and Abe (1977) found stages I-III in May and June; stages IV and V in June and July; and megalops from June to August. Takeuchi determined that stages were roughly 2 weeks apart. Stages I and II were only found in the surface layer (0-19 m), whereas stages III-V occurred in the surface and middle (20-50 m) layers. Temperatures ranged from 6° to 11°C at the surface and from 2° to 10°C in the middle layer. Along the West Kamchatka Shelf, stage I larvae were found late-April to May and stages II-V in June and July (Makarov 1967). In the EBS, stages I and II were found late-April to June; stage III, May and June; and stages IV and V and megalops in June (Armstrong et al. 1983[4]). Hair crab larvae in all three geographical areas were concentrated over bottom depths of 20-200 m, although some have been found in waters outside that range.

Abe (1977) reported that settlement of hair crab larvae near Hokkaido occurred in July, in waters 20-50 m deep, 5°-7°C, on sandy mud or fine sand. Juvenile crabs remained in that same general area for the next 1.5 years as they grew from 5.1 mm to about 44.5 mm RL[5] (40.2 mm CL) in eight successive molts. Ovigerous females were found in that habitat during the spring. Adult hair crabs moved offshore during July through September, as nearshore water temperatures gradually increased from 6° to 15°C (Abe 1977). Matui (1970) found adults at depths of 20 m in April to 130 m in autumn, offshore of eastern Hokkaido, but hair crab have been found at depths of 5-364 m in other areas around Hokkaido, the Kamchatka Peninsula, and Korea (Kawakami 1934; Sakai 1939). Hair crab were found on a variety of substrates, including sand, mud, gravel, rock, and broken shells, but sandy mud seemed to be most common (Kawakami 1934; Sakai 1939; Matui 1970; Abe 1977).

After settlement in July, hair crab metamorphose to first postlarval crab instars (C1) with a mean size of 5.2 mm RL (Abe 1977, 1982) (Fig. 3, top). External sex characteristics are evident at stage C2 and a mean size of 7.0 mm RL. By the following April, 12 months after hatching, the crab reach stage C7 at a mean length of 27.4 mm RL. Approximately 33 months after hatching, the crab reach maturity at C10 with a length of 55-60 mm RL (50-54 mm CL) (Abe 1977, 1982); however, hair crab males do not mate until 4 years of age and 70 mm RL (64 mm CL) (Sakurai et al. 1972). The smallest recorded male with mature spermatozoa was 41 mm RL (37 mm CL) (Hirano 1935). Molting frequency and mean carapace length are the same for both sexes through stage C9 (Abe 1977, 1982), however, after maturity males molt more frequently (Sakurai et al. 1972) and show greater growth per molt (Abe 1982) than females. Males begin to molt annually at about 55 mm RL (51 mm CL), once every 1-2 years (tending toward 2) in the size range 89-95 mm RL (81-87 mm CL), and biennially at sizes >100 mm RL (91 mm CL) and growth rate decreases with age (Yamamoto 1971). Males 65-105 mm RL (59-96 mm CL) experience a 10-25%

[4]Armstrong, D. A., L. S., Incze, D. L. Wencker, and J. L. Armstrong. 1983. Distribution and abundance of decapod crustacean larvae in the southeastern Bering Sea with emphasis on commercial species. Final Rep. to Natl. Oceanic Atmos. Admin., OCSEAP contract no. NA81-RAC-00059. Office of Marine Pollution Assessment, Alaska Office RD MPF24, P.O. Box 1808, Juneau, AK 99802.

[5]Japanese scientists have traditionally measured crab lengths from the notch between the rostral spines ("rostral-length", RL), whereas NMFS scientists measure from the right orbit ("carapace length", CL). We converted rostral lengths to orbit lengths with the following equations, determined for crab in the size range of 40-100 mm CL:

Males: $CL = -0.81 + 0.921\ RL$ $R^2 = 0.982$ $N = 122$
Females: $CL = -2.10 + 0.943\ RL$ $R^2 = 0.998$ $N = 8$

These equations have similar slopes but significantly different intercepts ($P < 0.05$). All NMFS crab measurements in this report are carapace lengths (CL). Japanese data are reported in original units (RL) and corresponding carapace lengths are also given for crabs >40 mm CL.

growth rate for carapace length (Yamamoto 1971) and females of 50 mm RL (45 mm CL) an 8-17% growth rate (Sakurai et al. 1972).

Molting periods for adult hair crab vary with sex and locality. In general, males distributed along the coasts of Hokkaido and Korea molt between the months of January and July (Yoshida 1940; Domon et al. 1956; Matui 1970; Sakurai et al. 1972) and females molt during the periods of April to June (Yamamoto 1966) or August to February (Sakurai et al. 1972).

Amphipods, anomurans, and isopods are important food items of the hair crab and peak feeding occurs at midday (Hirano 1935; Sakurai et al. 1972; Abe 1973). Hair crab are prey to fish species including various cottids (Sakurai et al. 1972; Abe 1973, 1982), salmon (Takeuchi 1972), and cod (June[6]), and are occasionally eaten by red king crab, *Paralithodes camtschatica*, (Cunningham 1969).

Hair crab migrate between shallow and deeper waters for mating purposes or in response to temperature changes (Yamamoto 1966; Sakurai et al. 1972). Primiparous females mate nearshore during winter, whereas multiparous females mate in deeper waters during autumn. Juveniles remain nearshore in water temperatures up to 15°C in late summer but adults move offshore. Hair crab also migrate along shore possibly to avoid increased densities (Hirano 1935; Abe 1977). Hirano reported that the longest straight-line migration of a tagged crab was 18 km over a 16-d period and the greatest migration speed was 1.39 km/day; however, the remaining 180 crabs recovered (442 tagged crabs released) within a 48-d period were at the site of release or within 7 km.

Hair crab have been fished in Japanese and Korean waters with the use of conical pots (Fig. 4), trawls, and gill nets (Matui 1970; Yamaha Fishery Journal 1981). In any month of the year fishing occurs at some location around Hokkaido; it occurs from about November to April offshore of southern Hokkaido (Kawakami 1934; Yamaha Fishery Journal 1981) and from March to December offshore of northern Hokkaido (Kawakami 1934; Matui 1970; Tanikawa 1971). Management measures have included area closures, total catch limits, pot limits, legal-size restrictions, and male-only restrictions (Matui 1970; Yamaha Fishery Journal 1981). Hirano (1935) and Kawakami (1934) believed that hair crab are especially vulnerable to fishing pressures owing to "localized" migratory behavior, low number and fecundity of females, and the extended breeding period. By 1980, about 10 t of hair crab were harvested offshore of Hokkaido every day, with 90% of the harvest transported live to fish markets throughout Japan (Iversen[7]), and the remaining 10% sold frozen.

U.S. fishermen began to land hair crab from the EBS in 1979 (Table 1). The majority of the commercial harvest has occurred incidental to snow (Tanner) crab (*Chionoecetes* sp.) fishing in the Bering Sea during the months of March through June, however, fishing season is not restricted. Only male crabs are landed. The Pribilof District (see Results for description of district) contributed 94-98% of the total Bering Sea catch during 1980-84. Harvested crabs averaged 105.7 mm CL and 0.91 kg in 1984. Landings ranged from 2 t in 1979 to a peak of 1,108 t in 1981. Modified, baited king and Tanner crab pots are normally used. Pribilof Islanders, however, conducted an experimental

[6]J. June, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. December 1982.

[7]R. Iversen, Regional Fisheries Attache, U.S. Embassy, Tokyo, Japan, APO San Francisco, CA 96503, pers. commun. August 1982.

TABLE 1.—Statistics of the U.S. commercial fishery of *Erimacrus isenbeckii* in the eastern Bering Sea (modified from Griffin and Dunaway, see text footnote 3). Mean length determined from port sampling, mean weight from landing records.

			Crab catch				Crab size	
Year	Vessels	Landings	number (× 1000)	Metric tons	Pots lifted	Crabs pot	Mean weight (kg)	Mean length (mm)
1979	11	16	2	2	9,908	0.2	0.95	111.8
1980	9	17	25	24	14,506	1.7	0.95	114.5
1981	67	192	1,127	1,108	172,695	6.5	1.00	104.8
1982	48	159	467	423	117,518	4.0	0.91	103.1
1983	52	161	575	550	84,346	6.8	0.95	103.2
1984	19	74	398	364	42,806	9.3	0.91	105.7

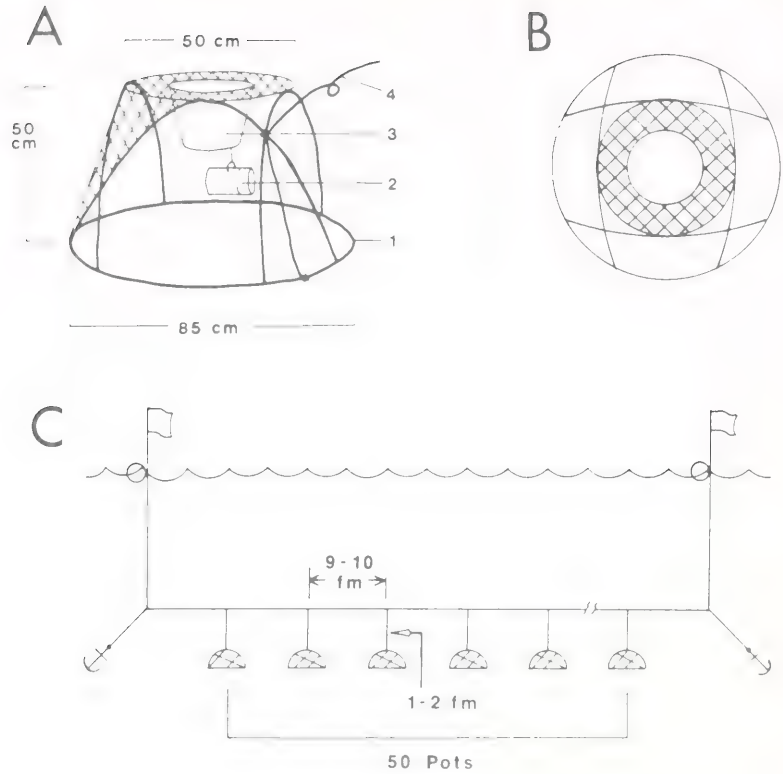


FIGURE 4.—Construction design and fishing method of Japanese hair crab pots. A, Side View: 1, lower ring of steel, upper ring and lateral bars of bamboo; 2, baitcan; 3, polyethylene cylinder entrance (28 cm top diameter, 25 cm bottom diameter, 19 cm high); 4, branch line attached to lateral bars and lower ring. Mesh shown only on top and one side. B, Top view: C, Longline method of pot fishing (fm = fathoms).

fishery for hair crab during the summer of 1980 with the use of small conical crab pots (Merculieff[8]). All hair crab harvested in the United States have been exported to Japan as live or whole-boiled product, and prices to fishermen have ranged from $0.50 to $1.60/lb.

MATERIALS AND METHODS

Hair crab were caught by NMFS during annual summer trawl surveys (primarily designed to assess the abundance of king crab, Tanner or snow crab, and ground-fish species) in the EBS from 1971 to the present, but detailed data on hair crab have been collected only since 1979. Fishing was conducted with a 400-mesh eastern otter trawl in 1979-80 and with an 83-112 eastern otter trawl in 1981-84; effective widths were 12.2 and 15.2 m, respectively (both nets were described by Wathne (1977)). Studies comparing the two nets showed no differences in size selection for king and Tanner crabs. We assumed the same for hair crab, which were too scarce for comparison. These differences in net widths have very minimal effect on the presentation of crab abundance, which is by order of magnitude (0-1, 1-10, 10-100 crab/nmi towed).

In all years, the survey area extended from the Alaskan coast out to approximately the 200 m isobath and included Bristol Bay and the Pribilof Islands area, where hair crab densities are usually greatest (Fig. 5). Only the northern limit of the survey area varied annually. Hair crab were also collected during NMFS cruises to the EBS in February of 1983 and 1985 and during an Outer Continental Shelf Environmental Assessment

[8]Merculieff, L. 1981. Final report on the Pribilof hair crab project. Unpubl. manuscr., 18 p. Tanadgusix Corp., St. Paul Island, AK 99660.

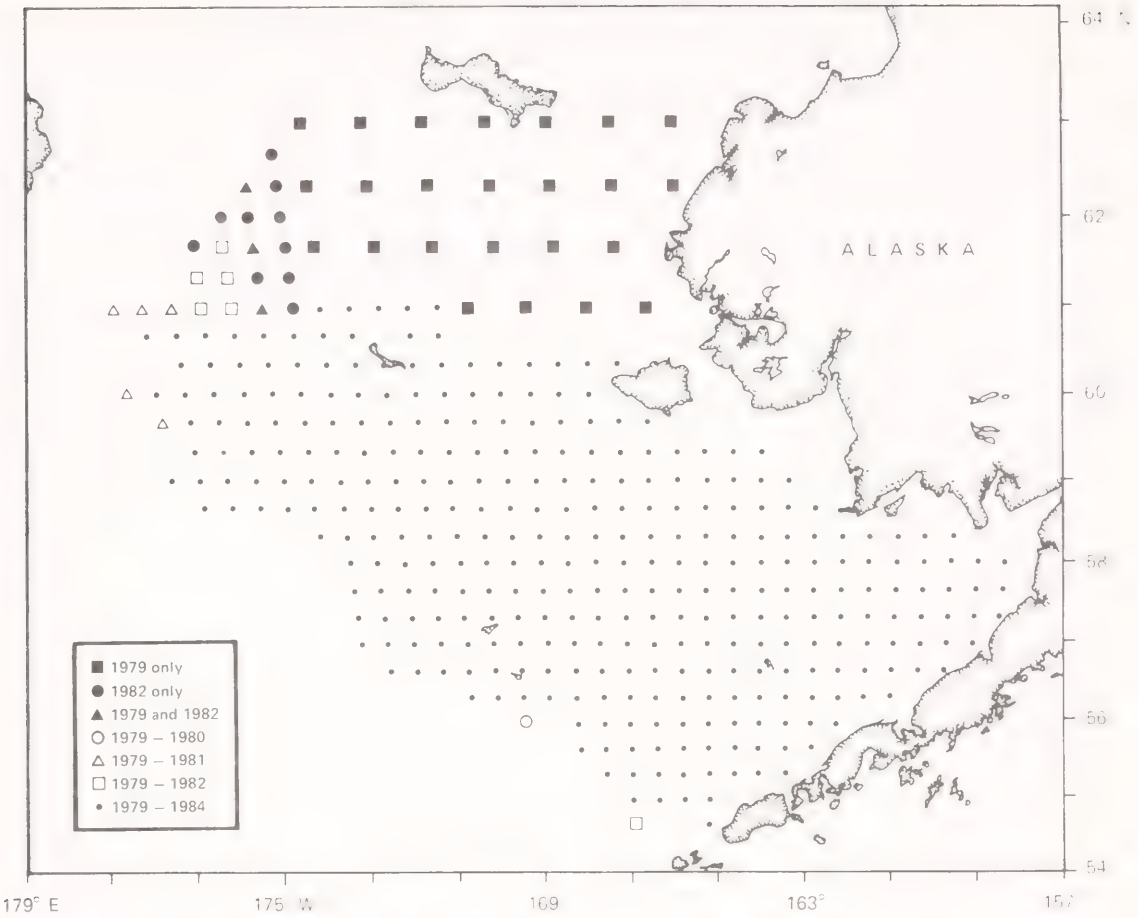


FIGURE 5.—Standard station pattern for NMFS eastern Bering Sea summer surveys, 1979-84. Actual stations occupied may have differed slightly from this pattern in any year.

Program (OCSEAP) cruise to the Pribilof Islands in May 1983. The seasons and durations of cruises are shown in Figure 6. Additional data concerning the NMFS summer cruises is contained in Otto et al. (1985, for the 1984 survey; similar documents are produced annually). Eastern otter trawl gear was used on all vessels throughout the 6-yr study period, except during the May 1983 OCSEAP cruise. On that cruise, either a 3.0 m beam trawl, 7.2 m try-net, or 1.2 m rock dredge were used to collect crabs, depending on bottom type determined from sediment samples taken with a Shipek bottom grab at each station. Fishing during both February cruises and the May 1983 cruise was conducted round-the-clock, whereas that during the summer surveys occurred only during daylight hours. Data collected during the February cruises and May 1983 cruise were not used in this report to determine distribution and abundance of hair crab in the EBS because of the limited area surveyed; only 1979-84 summer survey data were used for that purpose. Because different techniques were involved and no comparative fishing was conducted, catches of hair crab during the May 1983 cruise cannot be compared statistically with those from the summer surveys.

Tows were made in a systematic grid pattern with stations located 37 km (20 nmi) apart. During several years, extra tows were made in areas of higher hair crab abundance around the Pribilofs and in Bristol Bay, which increased the precision of population estimates during those years. Each tow lasted 0.5 hour and most were 2.2-3.3 km (1.2-1.8 nmi) long. Bottom temperatures were recorded with an expendable bathythermograph

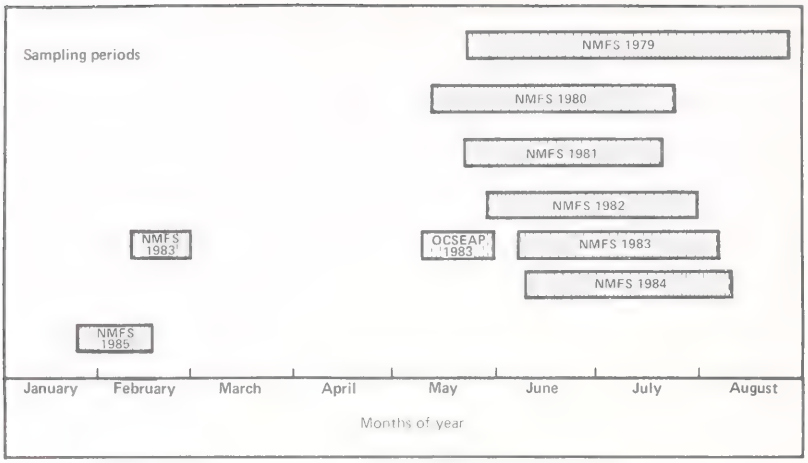


FIGURE 6.—Seasons and durations of sampling periods in the eastern Bering Sea, from 1979 through February 1985.

at as many stations as possible. After the catch was brought aboard, all species including hair crab were removed, counted, and weighed.

Carapace length of each crab was measured with steel vernier calipers to the nearest 1.0 mm from the rear of the right orbit to the middle of the posterior edge of the carapace (carapace length, CL). Carapace width (CW) was measured to the nearest 1.0 mm across the widest part of the carapace, excluding the lateral spines. Crabs were weighed on a triple-beam balance, and weights recorded to the nearest 1.0 g for crabs selected from a stratified size distribution. Shell condition was recorded as follows: molting (Drach's stages D_2 through E; Passano 1960), softshell (stages A_1 through B_1), new hard shell, old hard shell (probably skipped one annual molt), and very old hard shell (probably skipped several annual molts). Hard-shell conditions were graded subjectively according to the amount of epifauna on the carapace, color of carapace, and wear on the spines. A new hard-shelled crab carapace was relatively clean with no epifauna, reddish to yellowish brown, with sharp spines. A very old hard-shelled carapace, however, was usually darker brown in color and almost always had epifauna, and spines that were rounded or worn smooth. An old hard shell was intermediate between these two conditions, but in practice it was difficult to distinguish between new and old hard shell. The presence or absence of external embryos was recorded for all female crabs. Six ovigerous females caught by NMFS in the EBS, 1979-85, were preserved in 10% formalin and returned to the Kodiak NMFS laboratory for determination of fecundity. The entire clutch was removed from the crab, and the embryos dried, sieved to remove debris, and weighed to the nearest 0.1 mg. Three subsamples of embryos from each crab were weighed and counted. The total number of embryos was estimated by dividing the total clutch weight by the average embryo weight. For each of three crabs caught in 1980, diameters of 30 fixed embryos were measured to the nearest 0.1 mm under a stereomicroscope with an ocular micrometer, and average embryo diameters were calculated. Embryos were nearly spherical so no distinction was made between length and width. Other data were analyzed to determine distribution and abundance, sex composition, length frequency, molting periods, relative age according to shell condition, distribution by temperature and depth, and reproductive condition of females.

Population estimates were derived from trawl data using the area-swept technique (Alverson and Pereyra 1969) as described in Otto et al. (1985). The sampling variable was crab density, expressed as crabs caught per unit area swept, the latter equalling the product of net width and distance fished (determined with loran). High- and low-density strata were defined using the cumulative square root of frequencies method (Cochran 1963). Mean, total, and variance of crab density was determined within each stratum, and these combined for extrapolation to the survey area.

RESULTS

Distribution and Abundance

In the EBS, hair crab range from Bristol Bay west to about long. 174°00′W and north to St. Matthew Island at lat. 60°30′N (Fig. 7). Because so few juvenile and female hair crab were caught in NMFS surveys, the following information on distribution and abundance primarily concerns large males. Since fishery landings consist primarily of male crabs >89 mm CL, these are called "large", whereas "small" refers to male crabs <90 mm CL.

Within the survey area, the crabs are divided into eastern and western centers of abundance. The western group occurs primarily in the Pribilof District (Alaska Department of Fish and Game [ADF&G] statistical district; south of 58°39′N, and west of 168°00′W) and is most dense (>10 crabs/nmi trawled) immediately adjacent to the Pribilof Islands. Moderately dense concentrations (1-10 crabs/nmi trawled) surround the Pribilof high-density region, especially to the northeast and south. The eastern group occurs in the Bristol Bay District (south of 58°39′N and east of 168°00′W) and is centered along the northern shore of the Alaska Peninsula from western Unimak Island to about 160°00′W. This group is moderately dense, with areas of high density (10-100 crabs/nmi trawled) located near the western end of the Alaska Peninsula in 1979, and offshore of Unimak Island in 1981. Hair crab are scattered across the continental shelf between these two major population centers and in the Northern District (north of 58°39′N) in low densities (<1 crab/nmi trawled). As with large males, small males and females displayed distinct eastern and western concentrations, but very few were scattered between these two regions. Because of the more-or-less continuous distribution of hair crab across the EBS, we subsequently treat them as belonging to a single widespread population.

Population estimates have been made for hair crab only since 1979 (Table 2), and as previously mentioned, these reflect primarily the abundance of large males. From 1979 to 1981, the estimated population of EBS hair crab remained fairly stable between 22 and 24 million crabs. The population dropped 60% between 1981 and 1982, 35% from 1982 to 1983, and 30% more from 1983 to 1984, to a low of only 4.4 million crabs. (*Note added in proof*: Hair crab abundance has continued to decline to a total of 2.5 million crabs in 1986.) From 1979 to 1984, an average of 67% of the EBS hair crab occurred in the Pribilof District, 27% in the Bristol Bay District, and 6% in the Northern District. Although the total population size did not vary greatly from 1979 to 1981, the proportion of the population in the Pribilof District increased from 51 to 81%, while it decreased from 40 to 18% in the Bristol Bay District, and from 9 to 1% in the Northern District. By 1984, the population distribution was again similar to that of 1979. The population was very densely concentrated around the Pribilofs in 1981; however, since that time, the densities and range of hair crab in the EBS have declined greatly.

Females comprised only 8% (248) of the total catch of about 3,091 hair crab during the 1979-84 NMFS summer surveys. In contrast, females accounted for 40% (48) of the 120 hair crabs >40 mm CL caught during the survey conducted in the Pribilof Islands in May 1983, when fishing was conducted both day and night around the Pribilof Islands, with dredge, try-net and beam trawl.

Habitat

Male *E. isenbeckii* collected during the summer

TABLE 2.—Population estimates for *Erimacrus isenbeckii*, in the eastern Bering Sea, and proportions of the total population present in each statistical district. See text and Figure 7 for description of districts. Numbers are millions of crabs[1]. M = Male, F = Female.

	Pribilofs				Bristol Bay				Northern				Totals				Grand
Year	M	F	All	%	M	F	All	%	M	F	All	%	M	±%[2]	F	±%	total
1979	11.9	0.3	12.2	51	8.8	0.9	9.7	40	1.8	0.4	2.2	9	22.5	29	1.6	35	24.1
1980	15.1	2.3	17.4	77	3.6	0.7	4.3	19	0.8	0.1	0.9	4	19.5	47	3.1	138	22.6
1981	18.1	0.3	18.4	81	3.7	0.5	4.2	18	0.2	0.0	0.2	1	22.0	19	0.8	42	22.8
1982	6.3	0.1	6.4	67	2.3	0.2	2.5	26	0.5	0.1	0.6	6	9.1	22	0.4	56	9.5
1983	2.8	0.3	3.1	48	1.9	0.5	2.4	39	0.7	0.1	0.8	13	5.4	15	0.9	38	6.3
1984	2.3	0.2	2.5	57	1.2	0.1	1.3	30	0.5	0.1	0.6	13	4.0	16	0.4	48	4.4

[1]Numbers represent only crabs within the survey area and those large enough to be retained by the trawl, i.e. mostly large males (>89 mm CL)
[2]Two standard errors expressed as a percentage of the mean

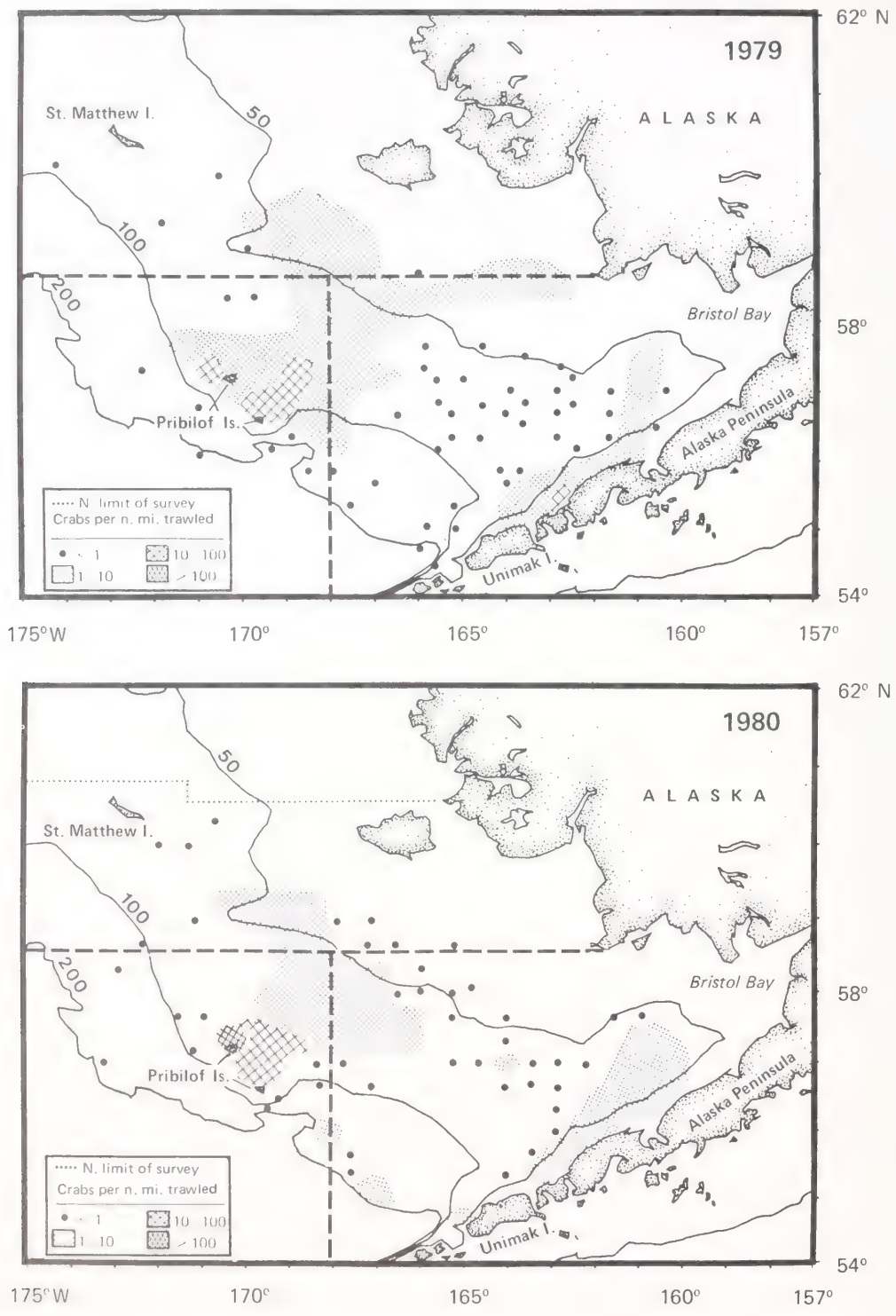


FIGURE 7.—Relative abundance of *Erimacrus isenbeckii* in the eastern Bering Sea, 1979-84. Depth contours are shown at 50, 100, and 200 m. Dotted line indicates the northern limit of the survey in each year. Dashed lines demarcate the Bristol Bay (south of lat. 58°39′N, east of long. 168°00′W), Pribilof (south of lat. 58°39′N, west of long.

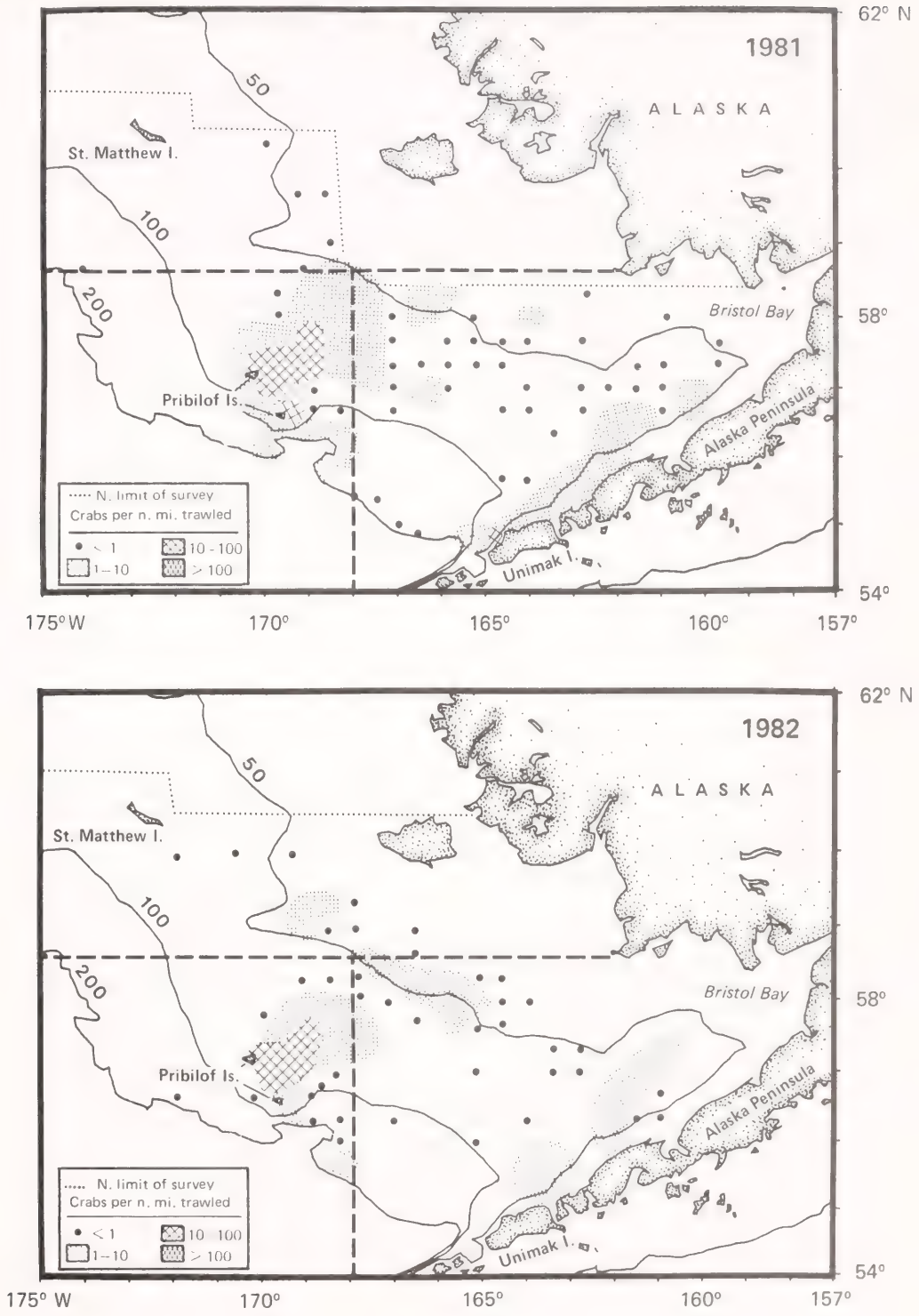
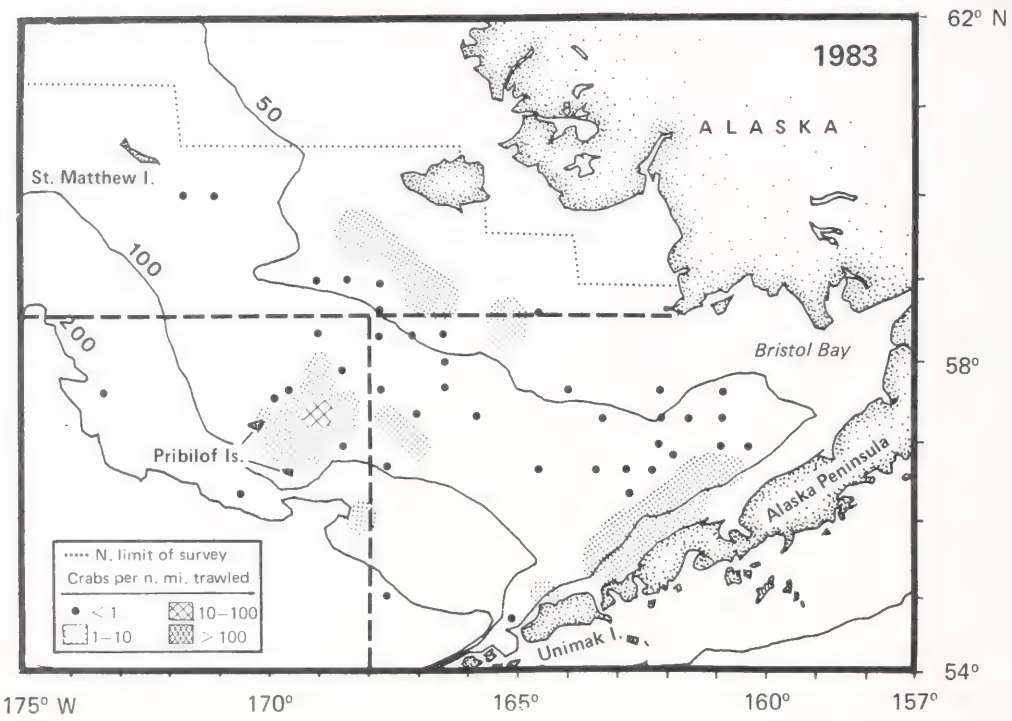


FIGURE 7.—*Continued*—168°00'W), and Northern (north of lat. 58°39'N) statistical districts. Densities expressed as crab per nautical mile trawled.



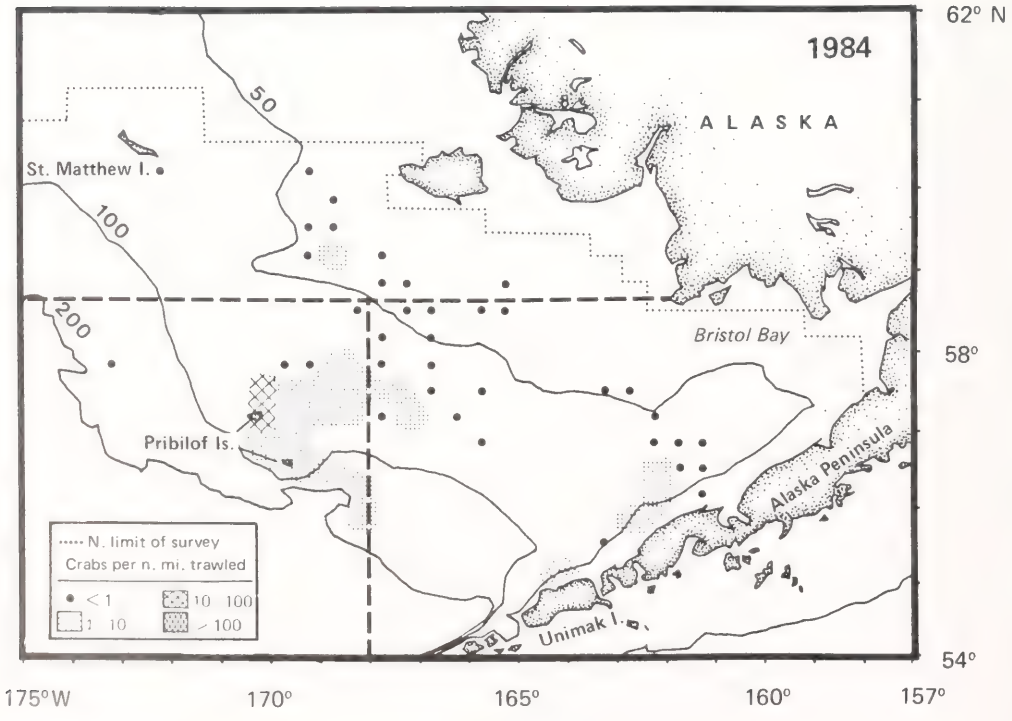


FIGURE 7.—*Continued*

surveys occurred at a mean temperature (weighted by crab abundance) of 3.4°C and depth of 65.6 m, although they ranged from −0.9° to 10.1°C and from 22 to 249 m depth. One male hair crab was found outside this range, at 401 m. The mean values for females were 2.4°C (range −0.9°-7.3°C) and 63.8 m depth (range 26-243 m). Results of a 2-sample t-test with unequal variances (Minitab "Twosample T" test; Ryan et al. 1976) indicated there was no significant difference ($t = 1.52$, df = 213, $P = 0.13$) between mean depths at which male and female hair crab were found; however, there was a significant difference ($t = 5.82$, df = 219, $P < 0.01$) between mean temperatures.

Data from the Pribilof Island study of May 1983 indicate that hair crab appear to prefer a heterogenous substrate as early juveniles, switching to sandy bottoms with increasing age. Among 120 juveniles <20 mm CL, 41% were on a substrate of gravel (less than about 1 cm diameter), polychaete tubes, and shell fragments, and small numbers were found in areas of large rocks, mud, or large shells. A substrate of medium or fine sand (usually containing shell fragments) was occupied by 58% of crabs in the size range <20 mm CL, 70% of 10 crabs in the range 20-40 mm CL, 94% of 73 males >40 mm CL, and all 48 females >40 mm CL.

Reproduction

The scarcity of juvenile and female hair crabs in NMFS collections prevented a thorough study of reproductive characteristics of the EBS population; only eight ovigerous females were caught from 1979 to 1985. The size at maturity of these crabs in the EBS is unknown, however, the smallest mature female caught by NMFS was 38 mm CL and had spermathecae filled with a viscous liquid, indicating it had been mated. The smallest female with empty egg cases caught by NMFS was a 42 mm CL old hard-shell crab. We follow Abe (1977) in assuming that the mean size at maturity for female hair crab is above 55 mm RL (50 mm CL).

Some female hair crabs collected during NMFS summer surveys were found with hard, proteinaceous plugs in the gonopores. The plugs were rootlike in appearance and formed a large, whitish, irregular-shaped protuberance outside the aperture (Fig. 8a). Each plug had a white, tapered stem that extended inward to the spermatheca (Fig. 8b). Some gonopores without plugs were closed by a flexible, swollen membrane (Fig. 8c) similar to the arthrodial membrane and continuous with the lining of the canal leading to the spermatheca. Some gonopores were open (Fig. 8d), owing to the flexible membrane having become flaccid.

Although the presence of closed pores was not associated with any particular shell condition of the female, plugs and open pores were. Plugs were present only in recently molted soft-shell crabs, while most females with open pores (28 of 30, or 93%) were new or old hard-shell crabs. Some females had only one plug, and 96% of these also had the other pore closed. During the May 1983 OCSEAP cruise, 40% (19) of the 48 large females (>40 mm CL) caught had plugged gonopores, 1 had new uneyed embryos, 4 carried eyed embryos that were in the process of hatching, and 11 carried empty egg cases. Of the 19 females with plugged gonopores, 89% (17) were new hard-shell crabs and 2 were newly molted soft-shell crabs.

Most female hair crabs caught carried no external embryos (Table 3A). Although few crabs with

TABLE 3.—Seasonality of egg bearing and molting in *Erimacrus isenbeckii* from the eastern Bering Sea. A) Percent of female crabs (actual number in parentheses) with embryos in each of 4 developmental stages. B) Percent of molting or soft-shelled crabs for each sex (total number of males or females caught shown in parentheses).

	February surveys		Summer surveys, 1979-1984, years combined			
	1983	1985	May	June	July	August
A. Condition of external embryos						
None	86(26)	93(14)	89(16)	88(109)	73(54)	38(12)
Uneyed	0	7(1)	0	0	1(1)	3(1)
Eyed	7(2)	0	11(2)	1(1)	0	0
Hatched	7(2)	0	0	11(14)	26(19)	59(19)
B. Frequency of molting or soft-shell crab						
Male	20.0(136)	0.0(56)	1.3(234)	2.0(1240)	3.1(1215)	0.0(154)
Female	30.0(30)	6.7(15)	0.0(18)	5.6(124)	18.9(74)	3.1(32)

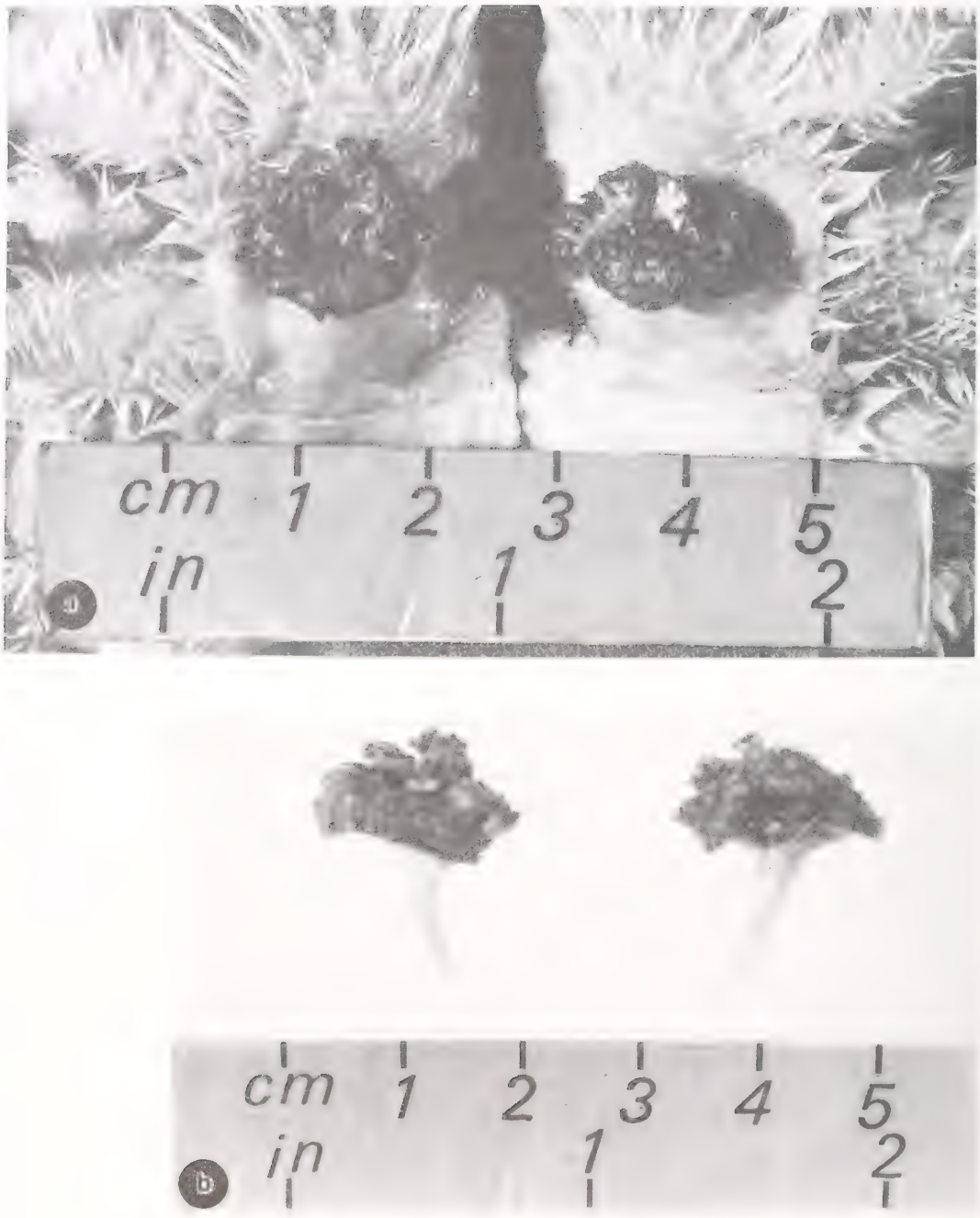


FIGURE 8.—Spermathecal plugs in formalin preserved female *Erimacrus isenbeckii*. a, ventral view of third thoracic sternite, with anterior towards the top of page, showing both gonopores with plugs; b, plugs removed from female crab; c, both pores closed (no plugs); d, both pores open. Plugs in live animals were whitish in color.

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embryos were caught, the highest proportions occurred in February and May. Empty egg cases became proportionately more abundant from June through August. The eight ovigerous females caught ranged from 56 to 87 mm CL. Fecundity estimates for six ovigerous females ranged from 34,000 to 160,400 embryos, averaging 0.9 mm in diameter (Table 4). Uneyed embryos were orange in color, whereas eyed embryos were dark brown.

Molting and Growth

Seasonality

Molting periodicity of hair crabs in the EBS is not well understood, owing to the lack of seasonal data. Summer cruises during 1979-84 turned up only three molting male crabs. Molting and soft-shell crabs comprised only 2.2% of males (65 crabs) and 8.9% of females (22 crabs) (Table 3B). Molting females were more abundant in July samples, but males showed no particular pattern.

Molting was much more apparent during the February 1983 cruise. Thirty percent (9 of 30) of female crabs were soft shell. Among the 136 males captured, 9% (12) were soft shell and 11% (15) were undergoing ecdysis. In contrast to the 1983 results, almost no molting was observed in February 1985. All 56 males captured were new hard shell or older, and only 1 (6.7%) of 15 females was soft shell.

In the EBS, based on the percentage of crab that we classified as new hard shell each year, an average of 79% of the large males (>89 mm CL), 95% of the small males (<90 mm CL), and 84% of the females appeared to have molted by the time the summer survey occurred.

Size Range

During the period 1979-84, 3,091 specimens of *E. isenbeckii* were captured in NMFS summer surveys, of which only 248 were females (Table 5). The average size of males caught was 96.1 mm CL

TABLE 4.—Estimated egg number and condition for six ovigerous female *Erimacrus isenbeckii* caught in the eastern Bering Sea from 1979 to 1985. Hyphens indicate no data taken.

Length (mm)	Date caught	Total[1] eggs	Egg condition	Egg color	Mean diameter[2] (mm)
65	9 82	107,900	—	—	—
69	5 80	103,400	uneyed	orange	0.86
74	9 81	113,600	eyed	—	—
79	7 85	160,400	uneyed	orange	—
82	5 80	99,800	eyed	dark brown	0.94
87	5 80	33,500	uneyed	orange	0.88

[1]Estimated from total dry weight of clutch (see methods).
[2]No obvious difference between length and width

TABLE 5.—Descriptive statistics of *Erimacrus isenbeckii* caught during NMFS surveys, 1979-84, in the eastern Bering Sea. Carapace lengths were measured from the right orbit.

	Mean	s	Range	Number measured
Males				
length (mm)	96.1	12.7	17-145	2,810
width (mm)	93.5	17.0	18-133	1,089
weight (g)	714.3	339.5	3-1574	703
Total males caught		2,843		
Females				
length (mm)	65.5	16.2	14-111	246
width (mm)	67.2	16.5	14-109	232
weight (g)	197.1	137.1	4-623	179
Total females caught		248		
Total caught		3,091		

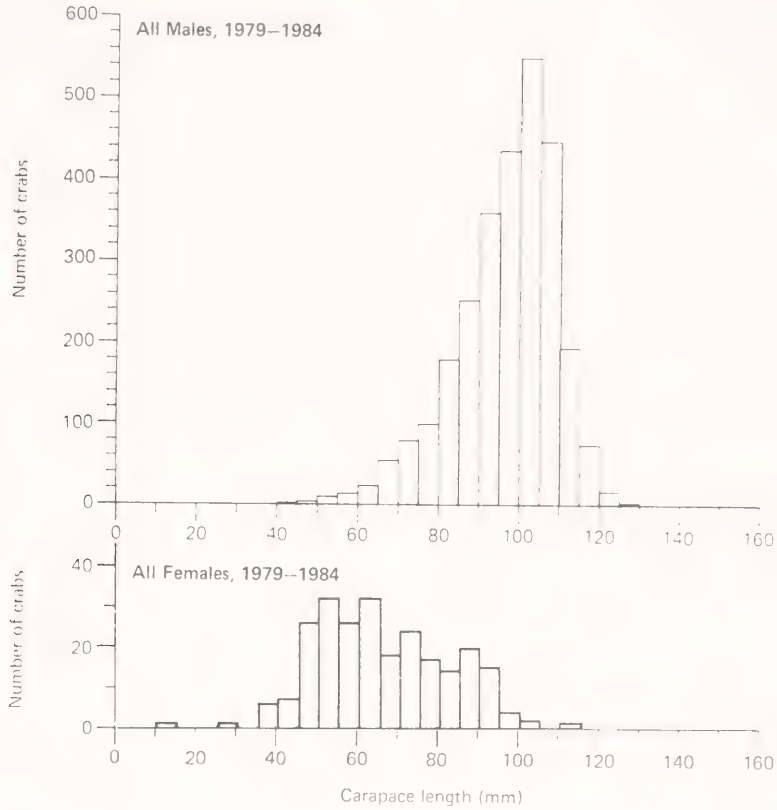

FIGURE 9.—Carapace length frequencies of *Erimacrus isenbeckii* collected during NMFS summer surveys in the eastern Bering Sea, 1979-84. Data for all 6 years were combined. Note scarcity of specimens below about 45 mm CL.

(range 17-145 mm); females averaged 65.5 mm CL (range 14-111 mm). Median values were 98 mm CL for males and 63 mm CL for females. The combined length-frequency distributions of male and female hair crab, 1979-84, are shown in Figure 9. In order to facilitate conversion between different methods of measurement, we calculated regression relationships between length, width, and weight (Table 6).

DISCUSSION

Distribution and Abundance

The decline of the EBS hair crab population occurred during the same time period (1980-84) in which substantial declines of red and blue king crabs (*Paralithodes camtschatica* and *P. platypus*, respectively), as well as two species of snow (Tan-

TABLE 6.—Regression relationships for length, weight, and width of *Erimacrus isenbeckii*, from the eastern Bering Sea. Length is carapace length from orbit.

	R^2	*n*
Males		
length (mm) = 2.28 + 0.974 width (mm)	0.945	1,087
L_n weight (g) = −7.24 + 3.02 L_n length (mm)	0.926	703
Females		
length (mm) = 1.87 + 0.938 width (mm)	0.969	231
L_n weight (g) = −6.73 + 2.86 L_n length (mm)	0.946	178

ner) crab (*Chionoecetes bairdi* and *C. opilio*) also occurred in the EBS (Stevens and MacIntosh 1985[9]). These events may be responses to common causes such as changes in the oceanographic environment of the Bering Sea, increased predation, or increased incidence of disease. A. K. Sparks[10] indicated that a presumptive viral infection was present in 13 of 20 hair crabs collected opportunistically in 1983, and in 2 of 3 examined from 1984 collections in the EBS. Although damage to the antennal gland in these infections suggest that the disease is fatal, this has not been proven. Fishery removals have ranged from <1% (before 1980) to a high of 11% (1983) of the estimated population of large males, which is probably underestimated (see Tables 1 and 2). Thus fishing pressure does not seem to have played a significant role in the population decline. A more plausible explanation of the decline in the hair crab population (and perhaps other EBS crab species as well) is that very large year classes may have been produced in the EBS in the late 1960's or early 1970's, recruited to the fisheries in the period 1977-80, and then declined to lower levels as these crabs succumbed to mortality. Historical data support this hypothesis for red king crab, and it may be applicable to hair crab as well as other species of crab.

Changes in the proportions of the hair crab population in various districts of the EBS (Table 2) may indicate that many crabs shifted from the Bristol Bay and Northern Districts into the Pribilof District and back again over the 6 survey years, or more likely, that the eastern and northern segments of the population began to decline several years before the Pribilof population, which may have been increasing until 1982. Bottom temperature did not seem to be an important factor in determining distribution of hair crab since there was no narrow range of temperature consistently associated with high catch rates.

The low percentage of female hair crab caught in the annual NMFS summer trawl surveys, compared with the relatively high percentage caught in the May 1983 survey, might be a result of gear selectivity, and possibly indicates that females were more abundant in shallow (<25 m) water or nearshore habitats that were not heavily sampled during the summer surveys. Low proportions of female hair crabs have also been captured during surveys around Hokkaido, where females comprised only 1-12% of the total catch (Kawakami 1934; Hirano 1935; Matui 1970). Hirano (1935) felt that the low numbers could be attributed to the small size of females in relation to mesh size of the net used for sampling, a preference by females for different habitats, or perhaps frequent burrowing. In a laboratory experiment, Hirano noted that females burrowed as deep as 13-15 cm for up to 4 days, whereas males burrowed for relatively short periods of time and usually so shallowly that the carapace protruded at the surface. Most (90%) of the adult females collected in the May 1983 survey were caught by trawl or try-net between the hours of 1900 and 0600. Abe (1973), however, found very little difference in the trawl catches of females between night (two 1-h tows at 2100 and 0330; 11 caught) and day (two 1-h tows at 0900 and 1500; 9 caught), although he did find that females were significantly more vulnerable to crab pots during the day (281 crabs/118 pots) than at night (46 crabs/115 pots). It is possible that increased activity of females during the day resulted in the higher pot-catch. During Abe's survey, females comprised 35% (347) of the total catch of 996 hair crab.

Depth, temperature, and substrate preferences appear to be similar for EBS and Japanese populations of hair crab, although maximum annual bottom temperatures in the EBS rarely exceed 12°C.

Compared with the distribution of juvenile and adult hair crab in the EBS, hair crab larvae were distributed primarily north and northwest of Unimak Island (Fig. 10) and concentrated in the upper 40 m of the water column, during surveys in the spring and summer of 1976-81 (Armstrong et al. fn. 4). Highest concentrations (over 5,000 larvae/100 m^2) occurred from Unimak Island north to about 55°30′N, mostly along the 50 m isobath. Low numbers (1-1,000/100 m^2) were scattered broadly over shelf and slope areas, but were more abundant along the 100 and 200 m isobaths. Sparse sampling occurred in the Pribilof Islands area during those surveys, but extensive sampling was conducted there in May 1983 (Arm-

[9]Stevens, B. G., and R. A. MacIntosh. 1985. Report to industry on the 1985 eastern Bering Sea crab survey. NWAFC Processed Rep. 85-20, 48 p. Kodiak Facility, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 1638, Kodiak, AK 99615.

[10] A. K. Sparks, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. May 1985.

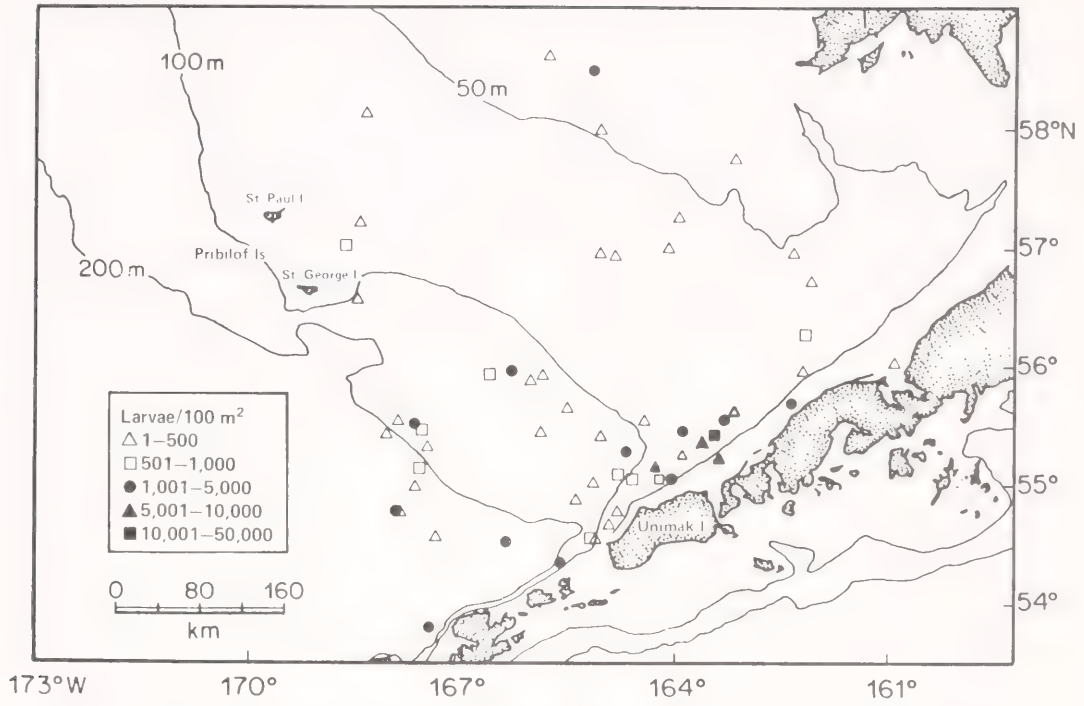

FIGURE 10.—Locations and densities of *Erimacrus isenbeckii* larvae collected in the southeastern Bering Sea, 1976-81. Locations where no larvae were found are omitted. With permission, from Armstrong et al. 1983 (see text footnote 4).

strong et al. 1984[11]). Highest concentrations (over 20,000 larvae/100 m^2 at one station) were found in waters 40-80 m deep, within about 24 km of St. Paul Island. Very few larvae were found near St. George Island.

Reproduction

The gonopore plugs found in female hair crab collected by NMFS resembled those described by Yoshida (1940) as having a "distal end that swells into an irregular form outside the aperture" and were of male origin (Morado[12]). The proximal tip of the plug extends to the spermatheca, as noted also by both Yoshida and Hirano (1935). The flexible, swollen membrane (Fig. 8c) that closed the aperture of some females is apparently not an exogenous plug, but a part of the female crab's body. The purpose of gonopore plugs is not known, but Hirano (1935) has conjectured that they serve to prevent copulation with other males during the period between the completion of copulation and spawning. They may also prevent degradation of the sperm from contact with seawater. Hartnoll (1969) reported that similar plugs have been observed in *Cancer irroratus, C. pagurus, Callinectes sapidus*, and *Carcinus maenas* and surmised that they prevent loss of sperm from female crabs which mated while still soft, or that they are a vestigial remnant of a hard sperm-case applied externally by more primitive ancestral brachyurans.

The following sequence of events is suggested by the observed associations between shell condition of female crabs and the presence or absence of gonopore plugs. After mating, the plugs loosen and slough off, either by mechanical abrasion (Yoshida 1940) or by dissolution from within as

[11]Armstrong, D. A., J. L. Armstrong, G. Jensen, R. Palacios, and G. Williams. 1984. Distribution, abundance, and biology of blue king and Korean hair crabs around the Pribilof Islands. Interim Rep. OCSEAP/OMPA contract No. 83-ABC-00066. Office of Marine Pollution Assessment, Alaska Office RD/MPF24, P.O. Box 1808, Juneau, AK 99802.

[12]J. F. Morado, Fisheries Research Biologist, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115, pers. commun. May 1982.

the female's ovaries mature (Hirano 1935), leaving the swollen membrane in place. The membrane eventually becomes flaccid, perhaps to allow egg extrusion. As the spawning period approaches, the spermatophores gradually break up and release spermatozoa. Fertilization occurs, either as the eggs are extruded (Kawakami 1934; Yoshida 1940) or afterwards, perhaps by contraction of the sperm sac and expulsion of the spermatozoa over the eggs (Sakurai et al. 1972). Our estimates of the number of external embryos carried by EBS hair crabs are in accordance with Sakurai et al. (1972, see Literature Review).

Molting and Growth

Molting frequency varies with age and sex of the crab. Because the percentage of recently molted male crabs declined with increasing size, the NMFS data appears to support Yamamoto (1971), who indicated that molting frequency of males decreases as size increases. Yoshida (1941) claimed that female hair crab molt every other year. Our data neither support nor refute this. However, old and new shell conditions are difficult to distinguish in hair crab, because shell discolorations and epibiota are uncommon. Thus, it is difficult to determine when a particular crab last molted. A higher frequency of molting in February (based on the 1983 data, Table 3B) for EBS hair crab tends to support the conclusions of Abe (1984[13]) and Sakurai et al.(1972) (Fig. 3) that hair crab molt and mate in winter, although the 1985 data did not. The second period of molting exhibited by female crabs in July tends to support the contention by Sakurai et al. that multiparous females molt and breed from August to November; however, females exhibited a low frequency of molting in August. Crabs of all sizes molted in both periods.

The effect of temperature on molting periodicity of hair crab is unknown. Mean bottom temperatures that were 2.5°C warmer in February 1985 than February 1983 for stations sampled for hair crab in both those years could have affected the onset of molting in 1985. Whereas in 1983, 22% of the hair crab caught were molting or in soft-shell condition, in 1985 only 1% were.

Abe (1982) determined the mean carapace length of 14 male and 13 female hair crab postlarval instars (Table 7) through length-frequency analysis of 10,547 individuals. For the first 9 instars, there was no difference in mean carapace length between males and females. However, after sexual maturity (i.e., sizes greater than about 55 mm RL or 50 mm CL) females showed less growth per molt than males, although growth increments decreased with age for both sexes. Abe plotted postmolt carapace lengths (L_{n+1})

[13]Abe, K. 1984. Reproductive cycle of hair crab. Unpubl. manuscr. Chief, Fisheries Resources Division, Hokkaido Wakkanai Fisheries Experimental Station, 5-4 Horai, 4-chome, Wakkanai, Hokkaido, 097, Japan. Presented at the hair crab conference, Yoichicho, Japan, January 31, 1984.

TABLE 7.—Mean carapace length (mm RL) for each postlarval instar of male and female hair crab, *Erimacrus isenbeckii*, (from Abe 1982), and calculated mean growth increment for the next molt.

Instar number	Mean length[1] (mm)		Percent increase		Calculated Orbit length (male)
	male	female	male	female	
C1	5.2		35		
C2	7.0		24		
C3	8.7		44		
C4	12.5		25		
C5	15.6		31		
C6	20.4		34		
C7	27.4		22		
C8	33.5		38		
C9	46.4		27	20	41.9
C10	59.1	55.9	24	18	53.6
C11	73.3	65.8	20	13	66.7
C12	88.2	74.1	17	13	80.4
C13	103.5	84.0	14		94.5
C14	117.5				107.4

[1]Lengths of females were same as males for instars 1-9

against premolt carapace lengths (L_n) and derived the following equations (not converted to CL):

Both sexes (<50 mm RL)	$L_{n+1} = -0.40 + 1.336\ (L_n)$
Males (>50 mm RL)	$L_{n+1} = 11.68 + 1.036\ (L_n)$
Females (>50 mm RL)	$L_{n+1} = 9.49 + 0.998\ (L_n)$

Abe (1982) plotted the regression of percent growth per molt on length, and estimated maximum lengths to be 125 mm RL (116 mm CL) for females and 177 mm RL (162 mm CL) for males. The largest hair crabs observed by NMFS in the EBS (Table 5) were smaller than these projections, as were those caught near Hokkaido by Abe (1982), who reported maximum lengths of 152 mm RL (139 mm CL) for males and 105 mm RL (97 mm CL) for females. Reportedly, female hair crabs from Hokkaido rarely reach a carapace length >80 mm RL (73 mm CL) (Sakurai et al. 1972). In contrast, over 20% of the females caught in the EBS were >80 mm CL. However, NMFS trawl gear caught few hair crab <40-50 mm CL, and juvenile and female crabs may occupy rocky nearshore habitat which cannot be adequately sampled by such gear.

The mean age of hair crab in the fishable population can be estimated from available data. Abe (1982) concluded that male crabs mature in their 10th postlarval instar, about 33 months after hatching, at about 60 mm RL (54 mm CL; Fig. 3). According to Yamamoto (1971), they would require one more annual molt to reach stage C11 in their fourth year. At this size, crabs may molt annually or biennially. Male crabs landed in the EBS fishery averaged 106 mm CL (116 mm RL) in 1984, or about stage C14 (Tables 1, 7). To attain this size would require 3 molts from C11, and these crabs would range in age from 7 to 10 years depending upon whether their last 3 molts were annual or biennial. If any failed to molt more than 1 year in a row, they would be age 11 at this size. Abe (fn. 13) (Fig. 3) indicated that male hair crab in Hokkaido waters reach similar sizes at the age of 6 years (assuming none skip molted).

Resource Potential and Management

Because of the great declines in abundance of the Bering Sea populations of *E. isenbeckii* from 1979 to 1984, this fishery will probably not be of great economic importance in the near future. If abundance increases in the future and prices remain adequate, this fishery might become lucrative, albeit on a small scale relative to other Bering Sea crab fisheries. The species could then probably support a small boat fishery in the Pribilof Islands. Hair crab are still in high demand in Japan.

The EBS hair crab fishery is not intensively managed. Fishing may occur year-round and is not limited by quotas. However, only males may be landed and gear is restricted to crab pots. There is no minimum size limit since the marketable size is large relative to the probable size of male maturity (about 54 mm CL), although the latter has not been adequately determined.

As a result of distribution and habitat differences as well as gear selectivity, the size-frequency distributions of NMFS collections have been largely unimodal with few juveniles and females in the catch. Thus, a thorough study of EBS hair crab reproduction and recruitment has not been feasible. Much useful information could probably be gained by systematic, year-round sampling of rocky heterogeneous habitats around the Pribilof Islands with appropriate gear such as rock dredges and beam trawls. Some data of this sort have already been collected by Armstrong et al. (fn. 11) and during other NMFS surveys, but are too limited to allow an improved understanding of growth rates, or the seasonality of molting and spawning of hair crab in the EBS. Further information on maturity, growth, and mortality is critical for informed management and will be necessary if this fishery gains importance.

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EXPLORATION FOR GOLDEN CRAB, *GERYON FENNERI*, IN THE SOUTH ATLANTIC BIGHT: DISTRIBUTION, POPULATION STRUCTURE, AND GEAR ASSESSMENT[1]

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ABSTRACT

Exploratory trapping for golden crab, *Geryon fenneri*, was conducted from 5 August 1985 to 21 February 1986 off South Carolina and Georgia. A buoyed system with strings of six traps (three side-entry Fathoms Plus and three top-entry Florida traps) was fished in six depth strata: 274-366 m, 367-457 m, 458-549 m, 550-640 m, 641-732 m, and 733-823 m. A total of 3,152 *G. fenneri* (2,661.9 kg) were collected at sampled depths between 296 and 810 m. The only other numerically important species caught was the jonah crab, *Cancer borealis* (864 individuals, 227.5 kg).

Catches of golden crab were highly variable between strata. Catch per trap increased from 1.6 crabs (1.67 kg) in the shallowest stratum sampled to a maximum abundance of 22.3 crabs/trap (18.04 kg/trap) in the 458-549 m depth zone. Catches abruptly declined in the deeper strata sampled.

Number of golden crab per trap (1.7:1) and weight per trap (1.6:1) in the Florida trap exceeded that in the Fathoms Plus trap for all completed sets. Traps yielded golden crab as small as 85 mm CW but the greatest proportion of crabs was >100 mm CW. Over 90% of all individuals exceeded 114 mm CW which is the minimum size of red crab, *G. quinquedens*, accepted for commercial utilization. Male golden crab were more numerous and larger than females.

Crabs of the genus *Geryon* (Brachyura: Geryonidae) are deepwater inhabitants of the Atlantic, Indian, and Pacific Oceans (Rathbun 1937; Monod 1956; Christiansen 1969; Manning and Holthuis 1981). Species reported off the United States in the western Atlantic and Gulf of Mexico include the red crab, *G. quinquedens* Smith, and the golden crab, *G. fenneri* Manning and Holthuis. At the time *G. fenneri* was described (Manning and Holthuis 1984), its geographic and bathymetric distribution included the continental slope off eastern Florida, the Florida Straits, and the Gulf of Mexico. An exploratory fishing effort in 1984 collected the first known specimens of golden crab off South Carolina[4], and it is now known that golden crab occur in waters off Bermuda (Luckhurst in press).

Both *G. quinquedens* and *G. fenneri* have been the target of limited and sporadic commercial fishing efforts off the east coast of the United States (Gerrior 1981), in the Gulf of Mexico. (Otwell et al. 1984; National Marine Fisheries Service 1986[5]), and off Bermuda (Luckhurst in press). Although much information is available concerning the biology and commercial fishery of red crab (summarized by Gerrior 1981), biological information on golden crab is more limited. Otwell et al. (1984) demonstrated exploratory trapping and processing techniques for golden crab from the Gulf of Mexico.

The initiation of a small commercial crabbing enterprise during 1984 in South Carolina yielded promising quantities of golden crab[6]. We began the present study to determine the fishery potential, compare trap designs, delineate bathymetric distribution, and describe the biology of golden crab in the South Atlantic Bight. This report documents results on catch rates, size and sex compo-

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[4]South Carolina Wildlife and Marine Resources Department, unpubl. data, courtesy Charles Wenner, Marine Resources Research Institute, Charleston, SC.

[5]National Marine Fisheries Service. 1986. Species profile: deep red crab, *Geryon quinquedens*, Smith and golden crab, *Geryon fenneri*, Manning and Holthius, 1984 from the southeastern U.S. south of Cape Hatteras, N.C. U.S. Dep. Commer. Natl. Mar. Fish. Serv., NOAA, Pascagoula Lab., Latent Resour. Rep., 17 p.

[6]H. Holley, commercial fisherman, Charleston, SC, pers. commun. 1985.

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sition of *G. fenneri* as a function of depth and trap type, and examines aspects of adult life history and reproductive biology of this species in the South Atlantic Bight.

METHODS

Cruises were made during the period from 20 June 1985 to 21 February 1986 on board the South Carolina Wildlife and Marine Resources Department (SCWMRD) research vessels *Oregon* and *Lady Lisa*, and the NOAA ship *Chapman*. All vessels were equipped with large capacity hydraulic systems and a heavy duty pot hauler.

Two commercially available trap designs were used to sample crabs. The Fathoms Plus[7] traps are oval (85 cm long × 66 cm wide × 30 cm high) and constructed of injection molded plastic. The trap has two side-entry funnels that can be enlarged by removing more of the plastic funnel's inner lip. The original, oval funnel opening is 10 cm × 20 cm. Both funnels were cut out to a maximum opening size of 14 cm × 22 cm. Traps were weighted with chain, making the total weight of each trap 11 kg. The Florida trap is an injection molded, high-impact plastic version of a Florida spiny lobster trap (82 cm long × 61 cm wide × 45 cm high). The top of the trap is constructed of wood lathing to provide a biodegradable escape panel. The top entrance funnel has adjustable panels and is 20 cm × 25 cm in the most open position, as fished throughout the study. Two strips of poured concrete in each end of the trap provided ballast, making the total weight of the trap about 22.7 kg.

Traps were baited with 1.2-1.6 kg of clupeids. Three Florida and three Fathoms Plus traps were alternately attached at 61 m intervals to 365.6 m of groundline. The groundline was constructed of 8 mm diameter Iceline, a dacron, polyethylene line that has a high tensile strength relative to its diameter. A small weight consisting of ~9.0 kg of chain was attached to one end of the groundline and an anchor (~25 kg) was attached to the buoyline end of the gear. Buoy lines were 366 m sections of 8 mm Iceline joined together to achieve at least a 2:1 ratio of line to water depth. Four inflatable net buoys and a spar buoy with radar reflector were attached to the buoyline.

Six depth strata were sampled between lat. 29°53.1′-32°20.0′N and long. 78°01.5′-79°24.8′W: 274-366 m (stratum 1), 367-457 m (stratum 2), 458-549 m (stratum 3), 550-640 m (stratum 4), 641-732 m (stratum 5), and 733-823 m (stratum 6). Three sets of six traps each were made approximately 1-2 km apart within a depth stratum over a 24-h period. Sampling locations for each set were selected by making fathometer transects of the potential fishing area to determine depth and bottom type. Because of bad weather and logistical constraints all strata did not receive equal effort (Table 1).

The first trap type on the groundline was randomly selected with trap type alternating until six traps (three of each type) were attached. The exception to this arrangement occurred in the deepest stratum (733-823 m) where only the Fathoms Plus trap was used.

Fishing duration was standardized at 20 hours; however, poor weather conditions and logistical considerations altered this. Average fishing duration within strata exceeded 17 hours (Table 1).

Bottom temperature was determined in each depth stratum by reversing thermometers. Bottom sediments were sampled by a geological rocket grab for each group of three sets made in an area. Sediments retrieved were frozen on board and examined under a microscope for gross characterization in the laboratory. Sampling depth and location were recorded at deployment of the anchor.

Decapod crustaceans in each trap were identified, counted, and weighed. Catches from damaged traps or those sets that moved due to currents were excluded from analyses of distribution and abundance, but were included in biological studies of size and sex composition. Each golden crab was individually sexed, measured to the nearest millimeter (carapace width, CW, distance between the tips of the fifth lateral spines; carapace length, CL, distance from the diastema be-

TABLE 1.—Mean, standard deviation, minimum, and maximum fishing duration of trap sets, for *Geryon fenneri*, within six strata sampled from August 1985 to March 1986.

		Fishing duration (h)			
Stratum	No. sets	$\bar{y}$	(*s*)	Min.	Max.
1	8	17.5	3.75	12.4	21.2
2	32	18.8	2.36	14.0	23.2
3	16	20.5	2.07	16.2	23.7
4	6	22.9	1.15	21.5	24.7
5	4	17.2	0.73	16.4	18.1
6	4	20.2	5.69	11.7	23.3

[7]Reference to trade names does not inply endorsement by the National Marine Fisheries Service, NOAA.

tween the rostral teeth to the posterior edge of the carapace, along the midline), and most were weighed to the nearest gram. The number of missing chelae and pereopods was recorded for each crab, as was molt condition and presence of chitinolysis and poecilasmatid barnacles, *Trilasmis inaequilaterale*, on the exoskeleton. Molt condition of *G. fenneri* was modified from criteria established by Beyers and Wilke (1980) for *G. quinquedens* (probably *G. maritae* Manning and Holthius) and consisted of five categories:

1) Hard - carapace at maximum strength, fouling by barnacles or chitinolytic bacteria minimal,
2) Hard old - carapace strong but heavily fouled by barnacles and abraded or blackened by chitinolytic bacteria,
3) Soft old - resorptive line along posterolateral sides of the carapace is weak; carapace heavily fouled as with hard-old condition,
4) Soft new - carapace soft or jellylike with no fouling, and
5) Hard new - carapace cracks under pressure and is not fouled.

Female *G. fenneri* were examined for evidence of egg extrusion and mating. Presence of eggs or egg remnants on pleopods and the size, shape, and physical condition of vulvae, as described by Haefner (1977), were noted. We examined seminal receptacles for presence of sperm or spermatophores and for relative size.

Ovaries from 72 of the 166 female *G. fenneri* captured were initially classified by relative size and color following the scheme described by Haefner (1977) for *G. quinquedens*. After gross classification of ovaries, tissues were removed for histological preparation and examination in order to describe ovarian structure and validate assigned ovarian stages. Tissues were fixed for at least 48 hours in 10% seawater formalin. After fixation, tissues were dehydrated, cleared, and embedded in paraffin. Sections were cut at 6-9 μm and were stained with Gill's hematoxylin and counterstained with eosin-Y. Oocytes from *G. fenneri* were measured using an ocular micrometer.

Testes and vas deferentia from three *G. fenneri* were fixed for 24 hours in 2.5% glutaraldehyde, rinsed in cacodylate buffer, and dehydrated in ethanol. Tissues were then critical-point dried, sputter coated, and examined using a Jeol JSM-35C scanning electron microscope (SEM).

RESULTS

Distribution and Relative Abundance

The 70 valid sets (416 individual trap observations) caught 3,152 *G. fenneri* (2,661.9 kg) at sampled depths between 296 and 810 m. The only other numerically important species caught was the jonah crab, *Cancer borealis* (864 individuals, 227.5 kg).

Catch per trap increased from 1.6 crabs (1.67 kg) in the shallowest stratum to a maximum abundance of 22.3 crabs/trap (18.04 kg/trap) in the 458-549 m depth zone (Fig. 1). Catches then abruptly declined with increasing depth. The absence of golden crabs in traps fished between 550 and 640 m appears to be related to unsuitable

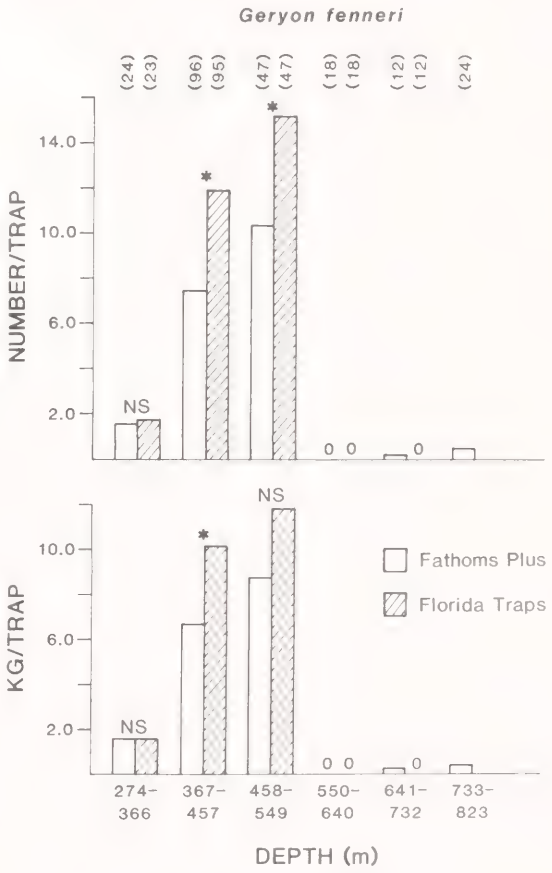


FIGURE 1.—Catch per trap of *Geryon fenneri* for six depth strata sampled. Effort (number of traps) is shown in parentheses. Statistical significance of catches between trap types, as determined by two sample *t*-test, is indicated by * ($P < 0.05$). NS indicates no significant difference in catch rates between the two trap types.

sediments at sites in this stratum since grab samples contained coral fragments and rubble. At shoaler locations where golden crabs were abundant, sediments were a mixture of soft silt-clay, molluscan shell fragments, and foraminiferan tests. Temperatures at sites where golden crabs were collected ranged from 7.14° to 9.15°C.

The number of golden crab per trap (11.4) and the weight of golden crab per trap (9.37 kg) in the Florida trap exceeded that in the Fathoms Plus trap (7.0 individuals, 6.16 kg) for all combined sets (Table 2). Statistical results by strata using the two-sample t-test or an approximate t-test when variances were heterogeneous (Sokal and Rohlf 1983), indicated significantly more crabs were collected with the Florida trap than with the Fathoms Plus trap from 367 to 457 m (stratum 2) and from 458 to 549 m (stratum 3) (Fig. 1, Table 2). Weight per trap was significantly different for the 367-457 m stratum only.

Size and Sex Composition

Male *G. fenneri* were significantly more numerous than females, outnumbering them by ~18:1. No ovigerous females were collected during the sampling period. Dominance of males was statistically significant for strata 1-3 (Table 3). In these depth strata, males were 20 times as numerous as females. In depths of 550-732 m, a male was the only crab collected. In the deepest stratum sampled (733-823 m), females significantly outnumbered males 2.9:1. Although the Florida trap caught significantly more crabs than the Fathoms Plus trap overall, no significant difference was noted in the number of female crabs between those two trap types (χ^2 test, $P > 0.5$).

The 3,217 golden crabs which were measured ranged from 85 to 193 mm in carapace width and weighed from 100 to 2,109 g. Average weight of male golden crab collected during the study was 927 g ($s = 373.448$, $n = 1{,}640$) while average weight of females was 443 g ($s = 289.385$, $n = 86$). Carapace width-frequency distribution for *G. fenneri* gave modes at 155 mm for males and 100 mm for females (Fig. 2). The largest crab collected measured 193 mm and weighed 2,091 g.

Linear least-squares and functional regression equations (Ricker 1973; Sokal and Rohlf 1983) relating carapace length and live wet body weight with width are in Table 4. Width-weight relationships were calculated from data on individuals that were not missing appendages.

Of the 3,183 golden crabs examined for missing appendages, 2.4% were missing one or both chelae. Pereopods were missing from 307 individuals (9.6%).

Examination of carapace width and weight statistics for each depth stratum showed that mean size of male *G. fenneri* was greatest for the shallowest (274-366 m) and deepest (733-823 m) strata sampled (Table 5). For females, however, mean carapace width and weight were greatest in the deepest zone. At depths of peak abundance, mean carapace width ($t_s = 4.70$, $P < 0.001$) and mean body weight ($t_s = 2.70$, $P < 0.01$) of male crabs were significantly greater in the 367-457 m than in the 458-549 m depth stratum. No signifi-

TABLE 2.—Results of t-test (T_s) comparisons of mean number and weight (kg) per trap for two trap types (FM+ and FLA) fished in each depth stratum for *Geryon fenneri*. Standard deviation is noted in parentheses; * indicates significance at 0.05 level.

	Number/trap			Weight/trap		
Stratum	FM+	FLA	T_s	FM+	FLA	T_s
1	1.6(1.92)	1.8(2.21)	0.14	1.66(1.912)	1.80(2.157)	0.14
2	7.5(5.96)	11.9(9.95)	2.16*	6.67(5.097)	10.02(7.651)	2.06*
3	10.4(5.08)	15.2(7.08)	2.22*	8.82(4.164)	11.84(4.752)	1.91
4	0	0	—	0	0	—
5	0.1	0	—	0.07	0	—
6	0.5(0.28)	—	—	0.43(0.321)	—	—
Total	7.0(5.98)	11.4(9.38)	8.51*	6.16(5.052)	9.37(7.078)	6.18*

TABLE 3.—Frequency of male and female *Geryon fenneri* within each depth stratum. Asterisks denote significant deviation ($P < 0.05$) from 1:1 by Chi-square analysis

	Strata (m)					
Sex	274-366	367-457	458-549	550-640	641-732	733-823
Male	84*	1,790*	1,165*	0	1	11
Female	3	91	41	0	0	32*

cant differences, however, were noted in mean carapace width ($t_s = 0.85$, $P > 0.05$) and mean body weight ($t_s = 1.48$, $P > 0.05$) of females from these same strata.

Of the two traps used, the Fathoms Plus trap caught larger and heavier golden crabs than did the Florida trap. Mean carapace width ($\bar{y} = 143$ mm, $s = 19.69$, $n = 1303$) of crabs in the Fathoms Plus trap was significantly larger than that of crabs in the Florida trap ($\bar{y} = 139$, $s = 20.21$, $n = 1914$) [$t_s = 5.478$, $P < 0.001$]. A statistically significant difference was also noted for mean weight (Fathoms Plus: $\bar{y} = 928$, $s = 366.77$, $n = 775$; Florida: $\bar{y} = 881$, $s = 377.69$, $n = 951$) [$t_s = 2.598$, $P < 0.001$].

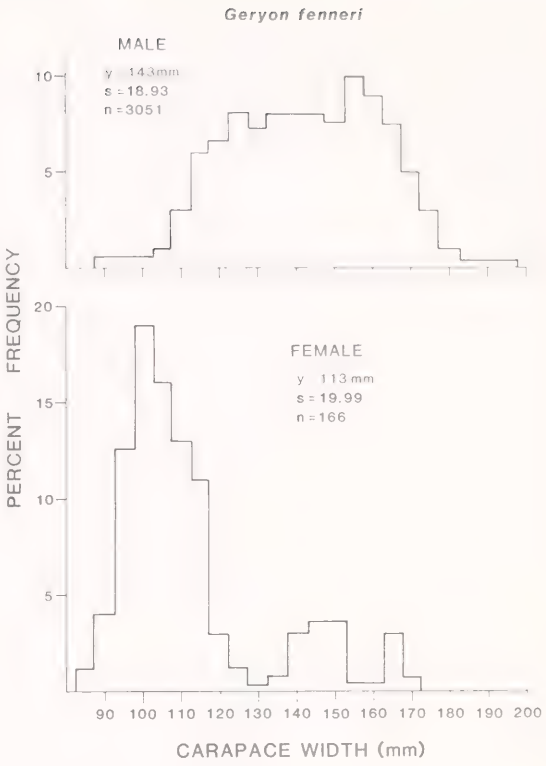


FIGURE 2.—Width-frequency distributions of male and female *Geryon fenneri* caught in traps. $\bar{y}$ = mean; s = standard deviation; n = number of individuals.

TABLE 4.—Least-square linear and geometric mean functional regression equations of carapace length (CL) and live body weight (WT) on carapace width (CW) for each sex of *Geryon fenneri*. Length and width units are millimeters while weight units are kilograms. All least square regressions were significant at $\alpha = 0.05$.

Sex	Least squares equation	n	r^2	GM functional equation
Male	CL = 9.5 + 0.9 CW	3,042	0.95	CL = −11.9 + 0.9 CW
	$\log_{10}$ WT = −4.74 + 3.54 ($\log_{10}$ CW)	1,453	0.94	$\log_{10}$ WT = −4.99 + 3.66 ($\log_{10}$ CW)
Female	CL = 4.0 + 0.8 CW	141	0.92	CL = 0.7 + 0.8 CW
	$\log_{10}$ WT = −3.97 + 3.14 ($\log_{10}$ CW)	74	0.91	$\log_{10}$ WT = −4.27 + 3.29 ($\log_{10}$ CW)

TABLE 5.—Size and weight statistics of male and female *Geryon fenneri* from sampled depth strata. $\bar{y}$ = mean; s = standard deviation, n = number of individuals.

Sex	Stratum (m)	Carapace width (mm)					Weight (g)		
		$\bar{y}$	Min	Max	s	n	$\bar{y}$	s	n
Male	274-366	156	117	186	14.4	84	1.064	339.15	84
	367-457	144	100	190	18.1	1.790	937	354.03	983
	458-549	140	88	193	19.9	1.165	884	373.47	561
	550-640	—	—	—	—	—	—	—	—
	641-732	139	-	–	—	1	809	—	1
	733-823	161	135	181	11.7	11	1,112	225.22	11
Female	274-366	105	92	113	11.2	3	189	80.88	3
	367-457	105	85	145	8.6	91	265	103.13	35
	458-549	104	85	137	9.7	41	228	70.06	16
	550-640	—	—	—	—	—	—	—	—
	641-732	—	—	-	-	—	—	—	—
	733-823	149	117	170	13.6	31	768	201.09	32

Reproductive Biology

We obtained satisfactory histological sections from 39 of 72 female golden crabs examined. From histological and gross examination we described four ovarian developmental stages: 1) early, 2) intermediate, 3) advanced, and 4) mature.

In the early stage of development, the slightly lobate ovary is very small, transparent to white in color, and bounded by fibrous connective tissue. Oocyte diameter ranged from 58 to 92 μm with a mean of 75 μm (Fig. 3A). Nuclei and nucleoli are readily apparent in the early oocytes, as are follicle or accessory cells which surround each

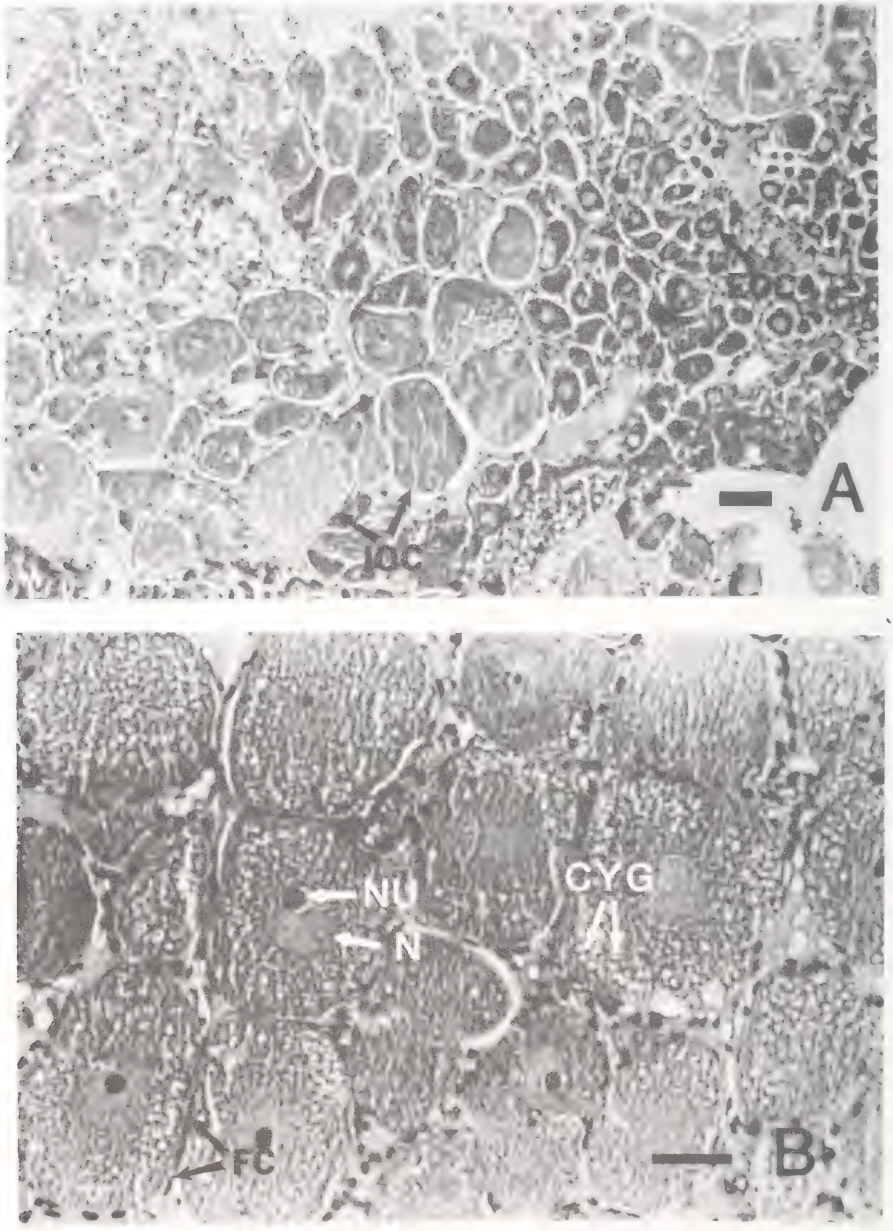
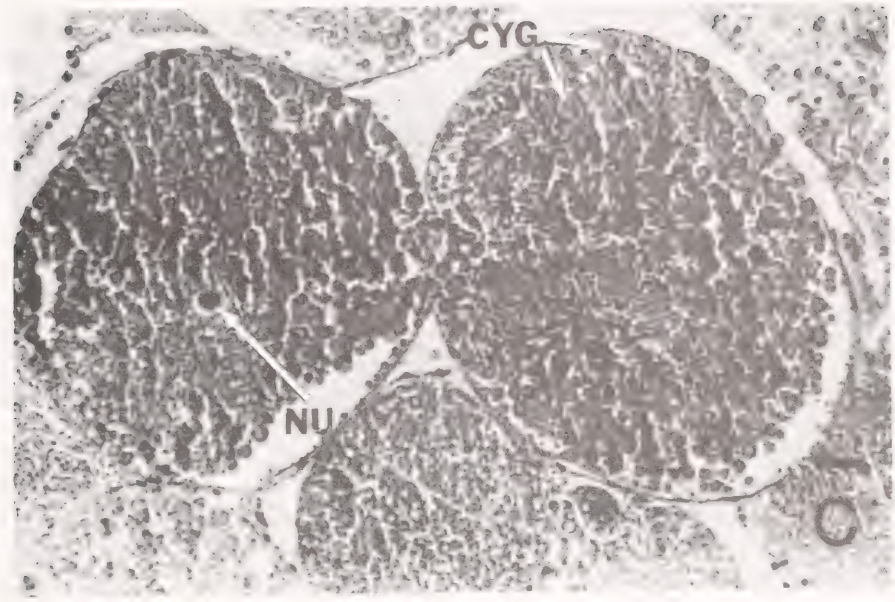


FIGURE 3.—Ovarian and testicular tissue of *Geryon fenneri*.

A. Ovarian tissue showing early (EOC) to intermediate oocyte (IOC) development. Oocytes range in size from 30 to 100 μm. Scale bar 60 μm.

B. Oocytes at the intermediate stage of development. Nucleus (N), nucleolus (NU), cytoplasmic yolk globules (CYG), follicle cells (FC). Oocyte size extremes are 100-125 μm. Scale bar 50 μm.



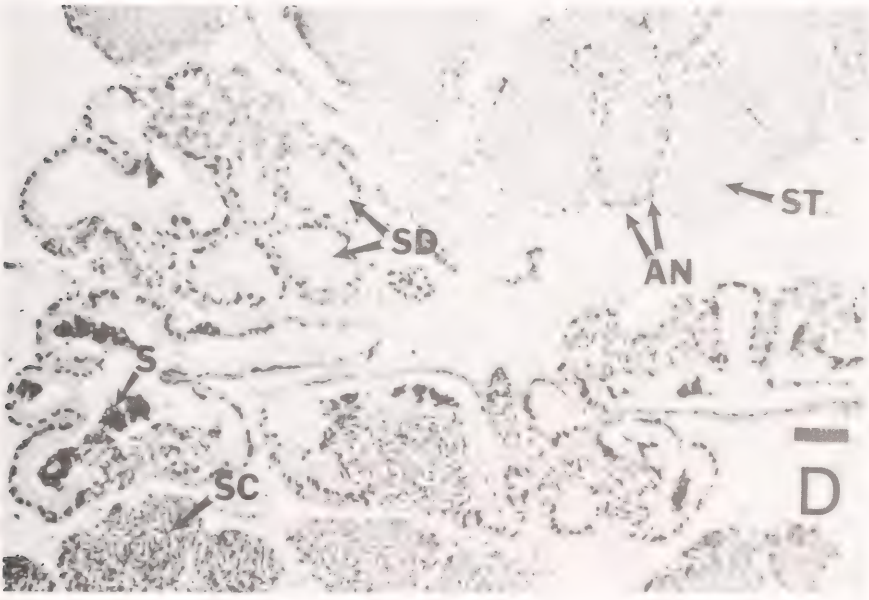


FIGURE 3.—*Continued.*

C. Oocytes in the advanced stage of development. Nucleolus (NU), cytoplasmic yolk granules (CYG). Oocytes 200-300 μm in size. Scale bar 30 μm.

D. A portion of a mature testis showing the seminiferous duct (SD) and testicular lobes containing spermatocytes (SC), spermatids (ST) and sperm (S). Accessory cell nuclei (AN). Scale bar 100 μm.

cell. In the larger oocytes, cytoplasmic vitellin globules indicative of vitellogenesis are present.

The intermediate stage ovary is yellow in color, has more pronounced lobation, and is larger than the early stage ovary. The diameter of oocytes ranged from 112 to 175 μm with a mean diameter of 145 μm. Most oocytes were undergoing vitellogenesis in this stage (Fig. 3B).

As the ovary matures to the advanced stage, the ovarian lobes become enlarged and the color becomes light orange to orange-red in color. The anterior portion of the ovary obscures the anterior hepatopancreas from dorsal view. Oocytes were 175-300 μm in diameter ($\bar{y}$ = 240 μm) and enlarge as vitellogenesis continues (Fig. 3C).

The mature ovary, brown to purple in color, is the dominant visible organ and obscures the hepatopancreas in dorsal view. Oocytes are filled with yolk globules and average 300-400 μm in diameter as vitellogenesis nears completion.

Size at sexual maturity was difficult to assess because of the small number of females collected. Overlap existed in the size of female *G. fenneri* in each stage of development.The carapace width of females in early ovarian development ranged from 85 to 116 mm ($\bar{y}$ = 104 mm, n = 27). Intermediate ovaries were present in females measuring 105-169 mm CW ($\bar{y}$ = 127 mm, n = 13) while advanced ovaries occurred at sizes from 110 to 136 mm CW ($\bar{y}$ = 123, n = 2). The 30 females with mature ovaries ranged from 97 to 169 mm CW ($\bar{y}$ = 141).

Five vulval forms were identified among the 142 females examined. Most of the females had immature vulvae (types a and b) suggesting that these crabs had not mated. The observed ovarian condition in a subsample (n = 26) of these females indicated that all had ovaries in an early stage of development (Table 6). Only one female (111 mm CW) with immature vulvae contained sperm in the seminal receptacles, indicating copulation had occurred. Type c vulvae were noted on two females, one with ovaries in early development and lacking sperm in the seminal receptacles while the other crab had mature ovaries and sperm present. Type e and f vulvae were found on the largest females collected, all of which had at least intermediate stage ovaries. Eight of the fourteen females with these vulval types whose seminal receptacles were examined had been inseminated.

Three male *G. fenneri* examined exhibited typical brachyuran reproductive morphology. The testes, which are dorsal to the hepatopancreas, were tubular and highly lobate. The testicular lobes, adjacent to the central seminiferous duct, contained spermatocytes, spermatids, and spermatozoa, suggestive of asynchronous development (Fig. 3D). In mature individuals, ripened spermatozoa were found in the seminiferous duct. Examination of the testes and vas deferentia by SEM revealed germ cells at various stages of development. Spermatids (Fig. 4A), surrounded by supportive tissue, were composed of a central nucleus framed in cytoplasm. With spermiogenesis, multiple projections or spikes form which are characteristic of developed sperm (Fig. 4A). Another portion of the same testis yielded a more advanced germ cell displaying well-defined cytoplasmic spikes (Fig. 4B). A sagittal section through the vas deferens revealed stellate spermatozoa (Fig. 4C), which had previously been embedded in this complex of supportive tissue (Fig. 4D).

TABLE 6.—Incidence of vulval type (after Haefner 1977) in relation to carapace width and gonadal condition of female *Geryon fenneri*. n = number of individuals examined.

Type	n	Carapace width (mm)	n	Gonadal condition
a	112	85-119	22	early
b	4	98-116	4	early
c	2	97-109	1	early
			1	mature
d	0	—	0	—
e	19	105-156	8	intermediate
			1	advanced
			9	mature
f	5	124-169	2	intermediate
			3	mature

Molt Condition and Fouling

Most (80%) of the 3,183 male and female *G. fenneri* were in the intermolt stage. Less than 1% of the 3,041 male golden crab showed evidence of having recently molted. The incidence of imminent or recently molted female golden crab was higher than that observed for males, with four individuals classified as premolt (soft-old) and two in the newly molted (soft-new) condition.

Most (95%) of the 3,183 *G. fenneri* examined for molt condition had blackened abraded areas on the exoskeleton, indicative of damage by chitinolytic bacteria. Exoskeleton damage was most prevalent on individuals in the intermolt (75%) and premolt (19%) condition.

DISCUSSION

Although the results of this study suggest that *G. fenneri* has a wide bathymetric occurrence in the South Atlantic Bight, the depth extremes for the species probably extend beyond those encompassed by our sampling design. Records of *Geryon* sp. and *G. affinis* (which were probably *G. fenneri*) from the Gulf of Mexico indicate a depth distribution of 365-1,455 m (Pequegnat 1970), while Luckhurst (in press) reported golden crabs from 786 to 1,462 m near Bermuda.

Although a broad bathymetric range for the species is likely, maximum abundance occurs between 367 and 549 m in our study area. This depth range coincides with that reported by Stone and Bailey (1980) for maximum trap catches of *G. quinquedens* along the Scotian Shelf and approximates the limits (320-530 m) determined by Wigley et al. (1975) by trawl and photographic methods to be most productive for that species off the northeastern United States.

Information on sediment composition taken coincidentally with fishing activities suggests that abundance of both *G. fenneri* and *G. quinquedens* is influenced by sediment type at these optimum depths. Our catches were highest on substrates containing a mixture of silt-clay and foraminiferan shell. In contrast, no golden crab were collected on rock and coral rubble bottom such as was encountered in the 550-640 m stratum. Other studies have described an association of *G. quinquedens* with soft substrates. Wigley et al. (1975) noted that bottom sediments throughout the area surveyed for red crab from offshore Maryland to Corsair Canyon (Georges Bank) consisted of a soft, olive-green, silt-clay mixture. If golden crabs preferentially inhabit soft substrates, then their zone of maximum abundance may be limited within the South Atlantic Bight. Surveys by Bullis and Rathjen (1959) indicated that green mud occurred consistently at 270-450 m between St. Augustine and Cape Canaveral, FL (30°N and 28°N). This same depth range from Savannah, GA to St. Augustine was generally characterized by Bullis and Rathjen (1959) as extremely irregular bottom with some smooth limestone or "slab" rock present. Our study indicates, however, that the bottom due east between Savannah and St. Catherines Island, GA at 270-540 m consists of mud and biogenic ooze. Further north from Cape Fear, NC to Savannah, bottom topography between 270 and 450 m is highly variable with rocky outcrops, sand and mud ooze present (Low and Ulrich 1983). Additional information on sediment type during future fishing efforts will be necessary before any validation of sediment preference by golden crab can be made.

The catch data for golden crab in our survey compares favorably with catch rates reported by Otwell et al. (1984) in the Gulf of Mexico. Although their study was not intended to assess the resource, they reported mean catch per trap values of 7.4-8.4 for the nested design fished between 210 and 340 fathoms. Information on catch rates of red crab from trap surveys and the fishery is perhaps more relevant to our study. Ganz and Herrmann (1975) reported an overall unculled mean catch per pot of 40-93 red crabs off southern New England; their study used four types of double parlor offshore lobster pots. An average catch of 26.8 red crabs per trap (conical-top entry) was reported in 360-540 m depths on the Scotian Shelf by Stone and Bailey (1980). The only available information on weight per trap was provided by Gerrior (1981) who found seasonal catch rates that ranged from a low of 8.4 kg in March to a high of 11.1 kg per pot in June. Although comparison of catch per unit of effort between these studies is questionable because trap type and fishing duration, as well as physical features of the sampling areas differ, catch per trap of golden crab in depths of maximum abundance off South Carolina and Georgia appears promising.

Comparison of catches (no./trap) between the Fathoms Plus trap and the Florida trap clearly indicate superiority of the latter for golden crab. These two traps also differed in the size and weight of individuals caught, with larger and heavier golden crab occurring in the Fathoms Plus trap. Advantages of the Fathoms Plus traps for commercial fishing operations would include their lighter weight, ease of handling, and stackable configuration which conserves deck space. Differences observed between traps may be related to trap design which affects success of entry and maximum catch (Miller 1980) or behavioral interactions which affect probability of capture (Richards et al. 1983). Although no studies have been done to evaluate behavior of *G. quinquedens* or *G. fenneri* in regard to traps, responses of the spider crab, *Hyas araneus*, and the rock crab, *Cancer irroratus*, to top and side entry traps were reported by Miller (1980). He found success of entry by *C. irroratus* was greater, escapement was reduced, and fewer agonistic encounters occurred in top entry traps. In a complementary study, however, *Cancer productus* had highest

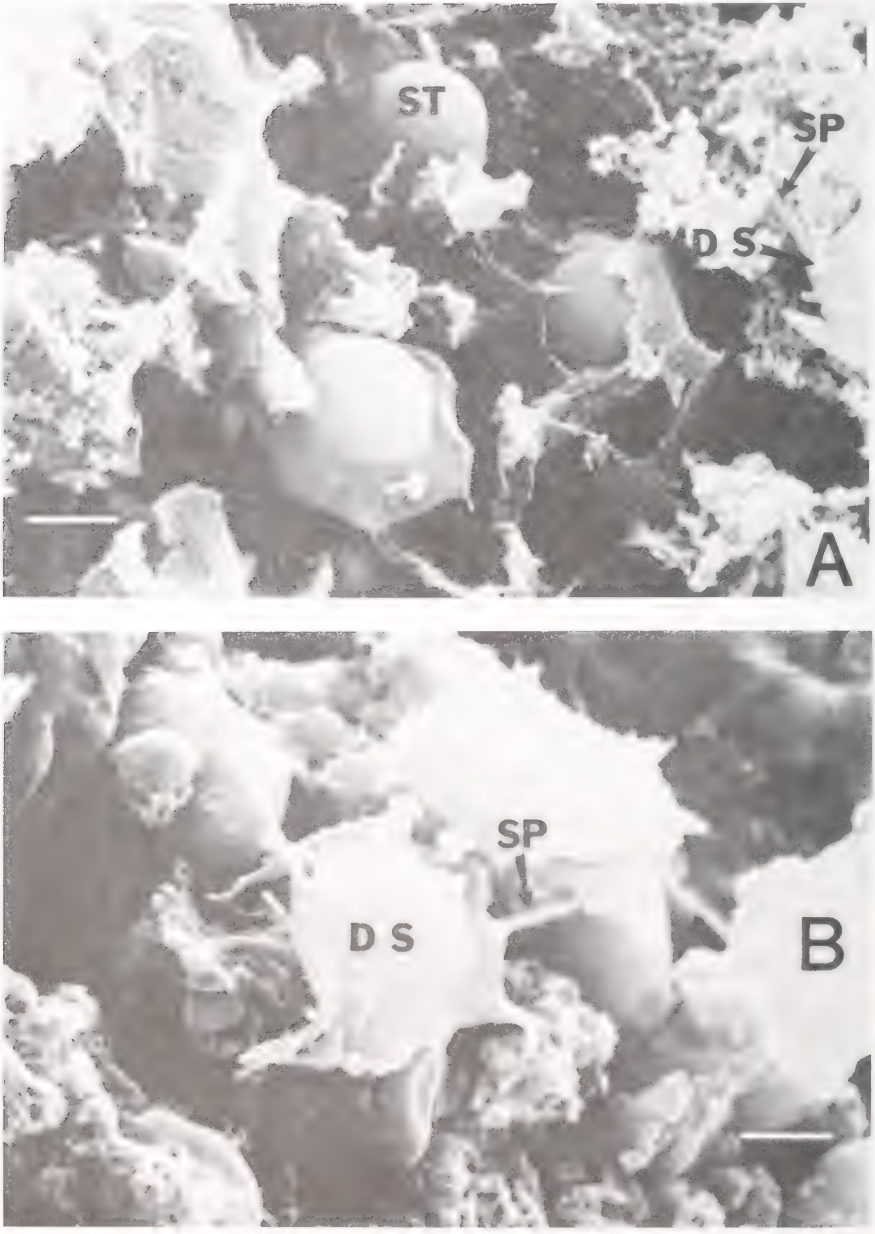


FIGURE 4.—Scanning electron micrograph of testis and vas deferens from male *Geryon fenneri*.
A. Testis: Maturing germ cells (spermatids, ST) surrounded by sustentacular tissue. Developing sperm (D-S), cytoplasmic spike (SP); × 3200. Scale bar 3 μm.
B. Testis: A developing sperm (D-S) possessing partial to fully formed cytoplasmic spikes (SP); × 3200. Scale bar 3 μm.

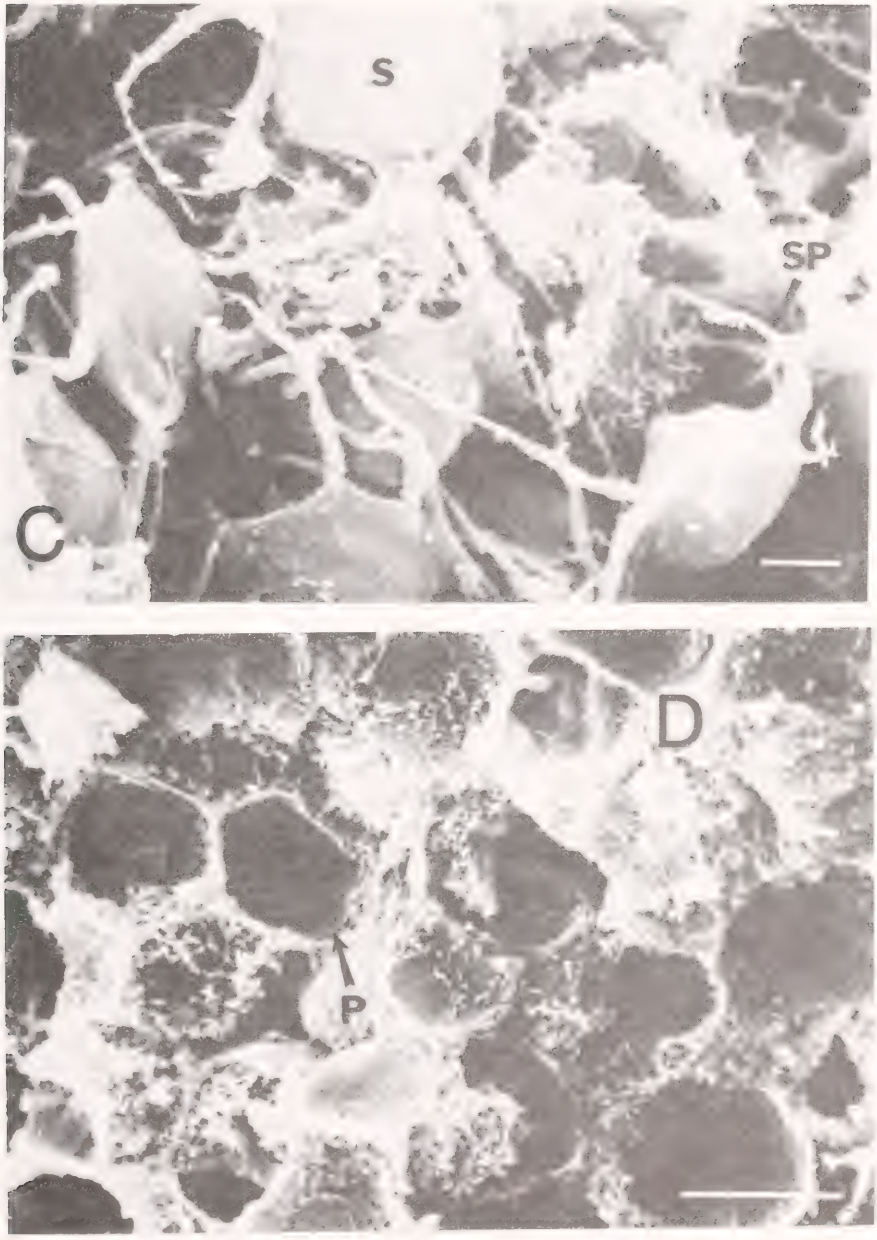


FIGURE 4.—*Continued.*

C. Vas deferens:- Mature multiple stellate sperm (S) showing cytoplasmic spike (SP); × 3840. Scale bar 2 μm.

D. Vas deferens: Pockets (P) within the vas deferens previously occupied by the mature stellate sperm; × 1600. Scale bar 10 μm.

success in entering a side entry trap whose entrances were parallel to the current (Miller 1978). Although our traps were deployed parallel to surface current, their orientation on the bottom relative to bottom current is unknown. We are assuming that golden crabs were successful in locating the entrance and were retained longer in the top entry Florida trap than in the Fathoms Plus trap. It is possible, however, that golden crab were equally or more successful in locating the side entrances of the Fathoms Plus trap but that escapement, especially of smaller golden crab, was higher. This would explain the capture of fewer but larger individuals by the Fathoms Plus trap.

The overwhelming dominance of males in this study contrasts with results reported in other geographic areas for golden crab. Luckhurst (in press) noted that sex ratio in his sample (n = 244) of *G. fenneri* from Bermuda waters was approximately 1:1. Otwell et al. (1984) noted that males tended to be more abundant at greater depths (>540 m) in the Gulf of Mexico; however, they cautioned that trap design may influence the percentage of male crabs caught. Commercial crabbers noted a decline in catch rates and number of male *G. fenneri* with increasing depth on the slope in the eastern Gulf of Mexico (National Marine Fisheries Service fn. 5). We also found increased abundance of females at greater depths, although our results are limited due to the small number of females collected. This is apparently not an artifact of sampling with only the Fathoms Plus trap in the deepest stratum since more females were collected in the Florida trap than with the Fathoms Plus trap when only strata 1-3 were considered. Segregation of the sexes by depth has been observed in several studies of *G. quinquedens*. Wigley et al. (1975) collected more female red crabs than males, but this dominance was limited to intermediate depths (320-503 m). Ganz and Herrmann (1975) similarly noted dominance by male red crab at depths >685 m off Rhode Island. This same pattern was noted for red crab in the vicinity of Norfolk Canyon where females were more abundant than males from depths <600 m (Haefner and Musick 1974; Haefner 1978). In Canadian waters, however, female red crabs were reported by Stone and Bailey (1980) to be considerably less abundant than males. Although they attributed this discrepancy to trap bias, another study in the same general area found females were present but highly contagious in distribution. Whether seasonal migrations related to mating or spawning occur as hypothesized by Wigley et al. (1975) for *G. quinquedens* remains to be substantiated. What is evident from our results is that male *G. fenneri* are dominant in depth strata where catch per unit of effort is highest.

Size-related distribution of *G. fenneri* with depth, similar to that reported for red crab, may occur in the South Atlantic Bight. We found the largest crabs in the shallowest (274-366 m) and deepest (733-823 m) strata. A clear trend of size-related up-slope migration such as Wigley et al. (1975) reported for *G. quinquedens* is not apparent, however, because of trap bias for capture of larger crabs of both sexes. Otwell et al. (1984) also noted no pattern in size of golden crab by depth for either sex. Tagging studies of red crab off southern New England provided no evidence for migration patterns and indicated instead that tagged crabs seldom moved more than 20 km from their site of release (Lux et al. 1982).

The size composition of golden crab from our study showed that crabs become trappable as small as 85 mm CW but that the greatest proportion of trapped individuals is >100 mm CW. Over 90% of all individuals collected exceeded 114 mm CW which is the minimum size of red crab accepted for commercial utilization (Wigley et al. 1975). A much smaller proportion (52%) of golden crab >114 mm was indicated in size-frequency distributions of trap-caught golden crab near Bermuda (Luckhurst in press). Although Otwell et al. (1984) did not present size and weight-frequency data for golden crab in the Gulf of Mexico, they found mean size of male crabs ranged from 155 to 163 mm with mean weight extremes of 1.07-1.15 kg, while females were smaller with mean CW ranging from 119 to 135 mm and mean weight extremes of 0.45-0.50 kg. These data and those from our study suggest that the average size of golden crab from the South Atlantic Bight and Gulf of Mexico is larger than the average size of red crab reported along the eastern United States and Canada. Wigley et al. (1975) reported average width of male *G. quinquedens* was 99 mm with an average weight of 413 g. Average width of all females from their study was 90 mm with a mean weight of 244 g. Comparisons of size composition between the two studies must be qualified, however, by a caveat that differences in sampling methods probably influenced sample statistics. The apparent larger size of golden crab may be better substantiated by maximum width and weight measurements, which for our study were

193 mm and 2,109 g, respectively. These values were markedly larger than those reported for red crab in the vicinity of Norfolk Canyon (Haefner 1978), off northeastern United States (Wigley et al. 1975), or the Scotian Shelf (Stone and Bailey 1980; McElman and Elner 1982).

The small number of females collected during the first year precludes any definitive statements regarding ovarian cycles or spawning patterns. Ovarian developmental stages are similar to those reported by Haefner (1977) for *G. quinquedens*. We also found his use of vulvae condition as an external indicator of copulation to be fairly reliable, but examination of the seminal receptacles for sperm or spermatophores provided the only true indication of mating. Tentative interpretations on ovarian development, vulval condition, and presence of seminal products suggest that females may become sexually mature at 97 mm CW. Haefner (1977) suggested that female *G. quinquedens* become sexually mature within the intermolt size of 80-91 mm CW.

A lack of ovigerous females in our first-year sampling effort could be indicative of a restricted spawning season similar to that reported for red crab (Haefner 1977; Wigley et al. 1975). Absence of ovigerous females from our samples, however, may be related to the small number of female golden crab collected.

Observations on molting and mating of a female (110 mm CW), which had been held in a refrigerated aquarium since February 1986 and had completed ecdysis in late May 1986, confirmed that female golden crab molt just before mating occurs. This behavior, as well as the observed premolt embrace, has been described for *G. longipes* (Mori and Relini 1979), although it has not been reported previously for either *G. quinquedens or G. fenneri.*

Stage of ecdysis is an important factor affecting meat condition and yield in golden crab. Crabs which have recently molted generally have a very poor meat yield and are not marketable[8]. Since most golden crab in the intermolt stage had blackened abraded areas or poecilasmatid barnacles on the exoskeleton, their presence was useful in distinguishing premolt from postmolt crabs which were brighter in color and had few abrasions.

[8]W. Lacy, Seafood Marketing Section, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. 1985.

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DIFFERENTIATION OF MITOCHONDRIAL DNA IN ATLANTIC HERRING, *CLUPEA HARENGUS*

I. KORNFIELD AND S. M. BOGDANOWICZ[1]

ABSTRACT

To investigate genetic relationships among spawning stocks of Atlantic herring, *Clupea harengus*, in the Gulf of Maine and Gulf of St. Lawrence, mitochondrial DNAs from ripe females at three localities were examined by restriction endonuclease analysis. Using seven variable restriction enzymes, mtDNAs from 69 completely characterized individuals produced 26 composite digestion patterns. The majority of individuals (65%) possessed composites which were common to two or more spawning localities; the other individuals displayed locality specific "unique" composites. Analysis of relationships among these unique composites suggested that some may have been derived from other areas. These results are not consistent with the idea that separate genetic stocks of Atlantic herring exist in the Gulf of Maine.

The relationships among discrete spawning stocks of Atlantic herring, *Clupea harengus*, are problematical. A large number of stocks and stock complexes are recognized throughout the eastern and western North Atlantic; these delineations are based largely on meristic characters, spawning time, and spawning location. Tagging studies in the western North Atlantic have shown extensive migration and mixing of stocks during nonreproductive periods (Creaser et al. 1984). More limited studies of spawning fish have demonstrated that some tagged individuals returned to their spawning locations (Wheeler and Winters 1984). Recent work has advanced the hypothesis that specific environmental attributes essential for growth and survival of larval herring largely determine where Atlantic herring will spawn (Iles and Sinclair 1982). The notion that spawning occurs near areas suitable for larval retention could explain the discontinuous or patchy distribution of spawning areas. Similarly, the occurrence of fall spawning and spring spawning Atlantic herring stocks may be a function of completion of larvae growth and metamorphosis constrained by resources within the larval retention area (Sinclair and Temblay 1984). There is thus a reasonable model to explain the existence of geographically or temporally discrete spawning stocks. However, the genetic structure among these different spawning groups is unresolved.

Implicit in the Atlantic herring stock concept is the idea that individual fish belong to defined groups by virtue of returning to specific spawning sites. If this is the case, there should exist high genetic continuity among individual Atlantic herring within stocks and relatively lower continuity among stocks. That is, genetic differences should be observable among stocks. Unfortunately, meristic characters useful for stock definition are under environmental influence and have a complex genetic basis. Electrophoretic characterization of allozyme variation should potentially permit identification of genetic discontinuities among stocks. However, despite the availability of a large number of polymorphic markers and adequate sample sizes, significant genetic heterogeneity among Atlantic herring stocks has not been demonstrated (Anderson et al. 1981; Kornfield et al. 1982; Grant 1984; Riviere et al. 1985). The inability of allozyme analysis to differentiate among herring stocks could occur for two alternative reasons. Herring stocks could have originated so recently that there has been insufficient time for stock specific allozyme variation to accumulate. Further, natural selection may be acting to homogenize allele frequencies that may characterize stocks. Thus, standard allozyme analyses may not be sufficiently sensitive to detect genetic variation which distinguishes stocks. Alternatively, herring stocks could be largely composed of individuals that do not return to natal spawning sites. Under this explanation, herring stocks would not represent discrete genetic groups but rather random assemblages of spawning individuals. Management of

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exploited herring stocks could differ dramatically depending upon which alternative is correct (MacLean and Evans 1981).

Restriction endonuclease analysis of mitochondrial DNA (mtDNA) has, in recent years, uncovered substantial genetic variation in natural populations (Brown 1983). The technique is potentially much more sensitive than conventional allozyme analysis for characterizing population structure and has been successfully exploited to discriminate groups not detectable with allozymes (e.g., Avise et al. 1986; R. W. Chapman unpubl. data). To further examine genetic relationships among herring stocks, restrictive enzyme digestion patterns of mtDNA were examined in individuals from three spawning localities in the northwestern Atlantic.

MATERIAL AND METHODS

Samples of fall spawning Atlantic herring were obtained from two discrete localities in the Gulf of Maine: Jeffries Ledge, MA (lat. 42°50′N, long. 66°30′W; 9 September 1984) and Trinity Ledge, NB, Canada (lat. 45°20′N, long. 65°30′W, September 1984; 30 August 1985). A sample of spring spawning Atlantic herring was collected from off Pt. Escuminac, Gulf of St. Lawrence, NB (lat. 47°01′N, long. 64°40′W; 12 May 1985) (Fig. 1). All Atlantic herring were collected during peak reproduction. Samples were frozen in the field and stored at −80°C for up to 6 months prior to analysis.

Lansman et al. (1981) provided a useful review of the application of mtDNA to population studies. mtDNA was prepared from egg tissue (11-15 g/female) by the rapid phenol extraction procedure of Chapman and Powers (1984). After the final chloroform extraction, mtDNA in the aqueous phase was precipitated in 95% ethanol in the presence of 3 M sodium acetate, dried under vacuum and dissolved in 10 mM Tris, pH 7.5.

FIGURE 1.—Collection localities for Atlantic herring. (1) Jeffries Ledge, MA; (2) Trinity Ledge, NB; (3) Point Escuminac (St. Lawrence), NB.

Samples were digested with 16 six-base restriction endonucleases (Table 1) under conditions recommended by suppliers (Bethesda Research Labs, New England Biolabs). Just prior to addition of restriction enzymes, samples were incubated with Ribonuclease A (RNase) at 60°C for 5 minutes and allowed to cool to 37°C. Restriction fragments were separated by horizontal electrophoresis in 1% agarose gels. *Hin*dIII digests of lambda DNA were used as molecular weight standards on all gels. Gels were stained for 60 minutes with 0.5 g L^{-1} ethidium bromide and destained for 30 minutes in 5 mM $MgSO_4$ prior to photography. The relative mobilities of mtDNA and lambda fragments were measured from photographs with a stereomicroscope. Molecular weights of restriction fragments were calculated from least squares third order polynomial regressions of log-transformed lambda fragment mobilities.

RESULTS

Restriction digests of mtDNAs prepared by the rapid phenol extraction procedure well resolved, repeatable digestion patterns (Fig. 2). Two enzymes, *Bam*H1 and *Sal*I did not digest the herring mtDNA molecule. Variant digestion patterns were noted for the majority of enzymes examined (Table 1) and were common both within

FIGURE 2.—Ethidium bromide stained agarose gel of mtDNA digestion patterns of Atlantic herring, *Clupea harengus* (lanes 2-8). Samples were digested with *Bst*EII (lanes 2, 3; phenotypes B, C), *Eco*RI (lanes 4, 5; phenotypes A, C), and *Bgl*II (lanes 6, 7; phenotypes A, B). Standard (lanes 1, 8) is a *Hin*dIII digest of lambda DNA.

TABLE 1.—Digestion patterns of Atlantic herring mtDNA produced by six-base restriction endonucleases[1]. Superscripts denote homologous fragments, measured independently.

*Apa*I						*Bst*EII					*Bgl*II			
A	B	C	D	H	I	A	B	C	D	E	A	B	C	D
8,800[a]	8,800[a]	7,200[e]	6,350	8,800[a]	7,350	11,830[d]	10,820[d]	15,160	12,200	11,700[d]	9,940	6,590[d]	14,000	6,600[d]
7,200[e]	6,100[c]	5,300	6,100[c]	7,200[e]	6,100[c]	4,670[a]	4,670[a]	1,150[c]	4,700[a]	3,650	4,130[a]	4,180[a]	1,990[b]	3,900
900[c]	960[d]	3,450	2,450[h]	1,100	2,450[h]	550[b]	1,160[c]	550[b]		1,340	1,990[b]	3,230[e]	1,270[c]	3,250[e]
	900[b]	900[b]	960[d]		900[b]		550[b]			550[b]	1,270[c]	1,960[b]		1,970[b]
			900[b]									1,220[c]		1,220[c]
16,900	16,760	16,850	16,760	17,100	16,800	17,050	17,200	16,860	16,900	17,240	17,330	17,180	17,260	16,940

*Dra*I		*Eco*RI			*Eco*RV				*Hin*dIII	*Kpn*I		*Pst*I
A	B	A	B	C	A	B	C	D	A	A	B	A
7,600	11,370	9,460[a]	14,020	9,400[a]	8,680[a]	8,200	8,600[a]	14,500	13,500	15,200	17,000	10,790
3,700	2,530[a]	4,220	3,130[b]	7,250	6,000	6,490	8,200	2,270[b]	2,820	1,910		5,850
2,570[a]	2,290[b]	3,010[b]			2,230[b]	2,030			1,000			
2,310[b]						1,000						
16,170	16,190	16,690	17,150	16,650	16,910	17,720	16,800	16,770	17,320	17,110	17,000	16,640

*Pvu*II			*Sac*I	*Xba*I	*Xho*I		*Xmn*I
A	B	C	A	A	A	B	A
7,480	12,840	13,600	9,800	5,350	14,000	16,500	7,940
5,590	1,550[a]	1,560[a]	7,300	4,880	2,690		3,780
1,580[a]	1,420[b]	1,400[b]		2,890			2,330
1,420[b]	850[c]			2,060			1,810
900[c]				2,050			1,320
16,970	16,660	16,560	17,100	17,230	16,690	16,500	17,180

[1]Two additional enzymes, *Bam*HI and *Sal*I produced no (or one) cuts.

and among population samples. For polymorphic restriction enzymes, all digestion profiles of variants were consistent with the hypothesis of single nucleotide substitutions. No mtDNA size variants, resulting from additions or deletions of DNA, and recently found in a number of fish groups (Bermingham et al. 1986; R. W. Chapman[2]), were observed.

The mean mtDNA genome size, found by averaging the sums of all digestion patterns (Table 1), was 16,990 bp (base pairs) ± 620 bp (SD). In quantifying molecular size from ethidium bromide stained agarose gels, two constraints must be noted. First, variation associated with measurement of fragment mobilities is inevitable. Because of the nonlinear relationship between fragment mobility and molecular size, slight measurement errors can produce large variations in estimated sizes, particularly for fragments with low mobilities. As a consequence, homologous cleavage fragments (those which consistently exhibit the same mobility on a single agarose gel) may yield different molecular size estimates, e.g., *Apa*I fragment "a", Table 1. Second, mtDNA cleavage fragments less than 500 bp could not be routinely scored on ethidium bromide gels because of their low absolute staining intensities and fluorescent background in this region (Fig. 2). Regardless of the above constraints, individual cleavage fragment phenotypes could be consistently determined.

Seven polymorphic restriction endonucleases (*Apa*I, *Bgl*II, *Bst*EII, *Eco*RI, *Eco*RV, *Pvu*II, and *Xho*I) were used to generate composite digestion patterns for individual Atlantic herring. Twenty-six unique composite digestion patterns were observed in 69 completely characterized individual Atlantic herring. The distribution of these composites with respect to spawning locality is given in Table 2; five common composites (nos. 1-5) were observed to occur at all three spawning localities.

Shared fragment similarity was calculated pairwise for all composites and was used to generate estimates of p, percent sequence divergence (Upholt 1977). Estimated sequence divergence among composites varied considerably, mean = 1.66% +/− 0.91 (SD), range 0.19% − 4.37% (Table 3). Phenetic relationships among composites were examined by UPGMA (Unweighted Pair Group Method of Arithmetic averaging) clustering (Sneath and Sokal 1973) of sequence divergence (Fig. 3). Two major clusters were noted: one involving three composites (5, 17, 26) and the other including all other composites. Composites from both clusters were present in all spawning populations.

A network of relationships among composites was constructed by connecting composites in increments of single site gains or losses to minimize the total number of restriction site changes required (Fig. 4). Sixteen equally parsimonious networks requiring 29 steps were generated. Composite number 1 can be considered central because it is the most common pattern observed and also occurs in the Eastern Atlantic (S. M. Bogdanowicz unpubl. data).

DISCUSSION

Based on the occurrence of geographically disjunct spawning groups and homing of some tagged individuals, it has been tacitly accepted that Atlantic herring stocks are reproductively isolated. The basic analytical premise of this study was that restriction endonuclease analysis

[2]R. W. Chapman, Chesapeake Bay Institute, The Johns Hopkins University, Shandy Side, MD 20764, pers. commun. December 1985.

TABLE 2.—Distribution of mtDNA composite digestion patterns in samples of Atlantic herring.

Composite designation	Composite mtDNA digestion pattern[1]	Jeffries Ledge	Trinity Ledge		St. Lawrence
			1984	1985	
1	AAAAAAA	5		2	5
2	AABAAAA	2	2	2	6
3	BAAAAAA	2		3	6
4	AABAAAB	1	1	3	1
5	ABAABAA	1	1	2	1
6	BABAAAA	1			
7	AABACAA			1	1
8	AAAADAB	1			
9	IAAAAAA				2
10	DAAAAAA				1
11	CAAAABA				1
12	BAEAAAA				1
13	HABAAAA				1
14	AAAAABB		1		
15	CAAAAAA		1		
16	BABAAAB		1		
17	ABABBAA		1		
18	ABBACAA			1	
19	AAACCAA			1	
20	IABAAAA			1	
21	AACAAAA			1	
22	BADAAAA			1	
23	CABAAAA			1	
24	AADAAAA			1	
25	ACDAAAA			1	
26	ADDABAA			1	
		13	8	22	26

[1]Letters (from left to right) are digestion patterns for *Apa*I, *Bgl*II, *Bst*EII, *Eco*RI, *Eco*RV, *Kpn*I, and *Xho*I (Table 1).

TABLE 3 —Estimated percent sequence divergence among mtDNA composites in Atlantic herring.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1	—	0.42	0.42	0.91	1.40	0.86	0.91	0.97	0.73	0.87	0.91	0.87	0.14	0.97	0.73	1.40	2.04	1.40	0.97	1.19	0.59	0.91	1.19	0.45	0.97	2.47
2		—	0.87	0.42	1.54	0.69	0.42	1.49	0.87	1.33	1.40	1.68	0.27	1.49	0.87	1.19	1.78	0.87	1.49	0.69	0.42	0.73	0.40	0.29	0.77	2.62
3			—	1.40	1.92	0.40	1.40	1.49	0.56	0.40	1.40	0.40	0.56	1.49	0.87	0.87	2.62	1.92	1.49	1.00	1.06	0.42	1.32	0.91	1.49	3.09
4				—	2.62	0.87	0.91	0.97	1.40	1.92	2.47	1.92	0.73	0.97	1.78	0.42	3.47	1.40	1.74	1.19	0.91	1.63	0.87	1.12	1.74	3.46
5					—	2.90	2.62	1.49	2.32	2.90	3.09	2.90	1.92	3.31	2.32	3.76	0.42	1.54	1.89	3.38	2.62	3.61	2.90	2.47	2.80	0.73
6						—	0.56	2.04	0.69	0.82	1.92	1.13	1.00	2.04	1.32	0.40	3.24	1.33	2.04	0.53	0.87	0.56	0.82	1.06	1.63	3.76
7							—	1.74	1.40	1.92	2.04	1.92	0.73	2.17	1.40	1.40	2.47	0.42	0.97	1.19	0.91	1.63	0.87	1.12	1.74	3.47
8								—	1.89	2.04	2.64	2.04	1.49	0.32	1.49	1.49	2.64	2.32	1.42	2.47	1.74	2.17	2.04	1.58	2.32	3.16
9									—	0.40	1.06	1.00	1.19	1.89	0.87	1.19	3.09	1.92	1.89	0.13	1.40	1.06	1.00	1.26	1.89	3.61
10										—	1.19	1.13	1.33	2.04	1.00	1.33	3.24	2.46	1.63	0.53	1.19	0.56	1.13	1.06	1.63	3.24
11											—	2.32	1.78	1.34	0.42	3.09	3.47	2.62	2.17	1.92	1.63	2.04	0.87	1.49	2.17	4.04
12												—	1.33	2.47	1.33	1.33	3.24	2.46	2.04	1.46	1.19	0.87	1.81	1.40	2.04	3.76
13													—	1.49	0.87	1.19	3.09	1.19	1.49	1.00	0.73	1.40	0.69	0.91	1.49	3.09
14														—	1.49	1.12	3.73	1.89	2.32	2.47	1.74	2.17	2.04	1.58	2.32	4.37
15															—	1.54	2.18	1.92	1.49	1.33	1.06	1.40	0.40	0.91	1.49	3.09
16																—	3.09	1.92	2.80	1.00	1.40	1.06	1.33	1.63	2.32	4.19
17																	—	2.18	2.64	4.33	3.47	4.04	3.76	3.89	3.73	1.26
18																		—	1.49	1.68	1.40	2.18	1.33	1.63	1.89	1.78
19																			—	2.47	1.74	2.17	2.04	1.58	2.32	3.16
20																				—	1.54	1.19	0.82	1.40	2.04	3.76
21																					—	1.26	0.87	0.77	1.34	2.95
22																						—	1.54	0.45	0.97	2.47
23																							—	1.06	1.63	3.24
24																								—	0.47	1.89
25																									—	1.73
26																										—

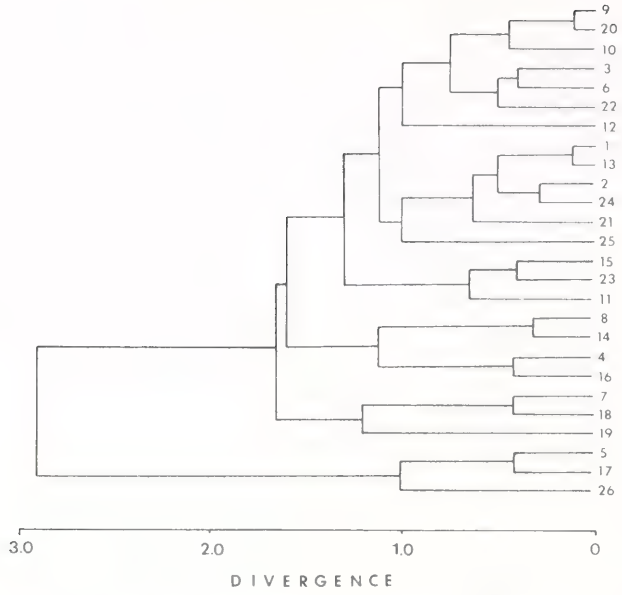

FIGURE 3.—Phenetic relationships among mtDNA composite cleavage patterns of Atlantic herring. Estimates of sequence divergence were clustered by UPGMA.

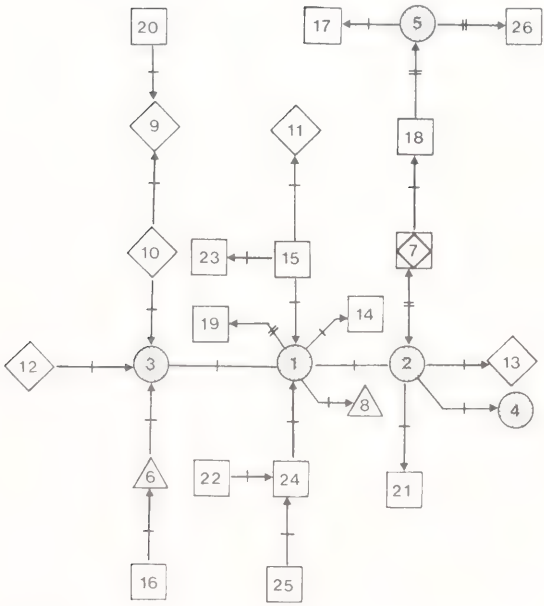

FIGURE 4.—Cladistic relationships of 26 composite cleavage patterns of Atlantic herring mtDNA. Composites are connected parsimoniously to minimize the number of restriction site changes required. Shaded numbers refer to composites observed at all three spawning locations. Crossbars on connecting lines indicate minimum number of site changes required to connect adjacent composites; arrows indicate direction of site losses. Locality symbols: square - Trinity Ledge; triangle - Jeffries Ledge; diamond - St. Lawrence.

of mtDNA should have been able to differentiate among such reproductively isolated populations. However, the spawning groups studied were not fully distinguishable by composite mtDNA digestion patterns generated by six-base restriction endonucleases; no absolute stock markers were present. Six of the twenty-six composite designations, representing more than 65% of all individuals, were shared by at least two geographically distinct spawing groups.

The occurrence of common composites in all spawning populations could occur for at least two reasons: First, commonality could reflect recent and/or ongoing gene exchange among populations. Consistent with this idea, there is no association between frequencies of common composites (nos. 1-5) and spawning locality (G = 6.29, p 0.5, Sokal and Rohlf 1981). As is generally acknowledged, small numbers of individuals migrating among populations are sufficient to homogenize different groups (Allendorf 1983). The absence of two common composites (1 and 3) in the 1984 Trinity Ledge sample might be due to the stochastic effect of small sample size, though this observation could also imply some element of temporal instability in composition. Second, and alternatively, these common composites could represent ancestral mtDNAs which were widespread prior to any genetic isolation of populations. That is,

the occurrence of common composites need not imply current gene exchange (Avise et al. 1984; Neigel and Avise 1986); population sizes are sufficiently large to support the co-occurrence of common ancestral composites and their derivatives.

The presence of 20 composites which were specific to spawning groups suggests that there may be some degree of genetic isolation among stocks. Given the limited number of individuals sampled, it is difficult to know whether "unique" composites are actually restricted to specific stocks. For example, rather than increasing the abundance of previously observed unique composites, the second sample from Trinity Ledge generated additional composites. There is thus little indication that "unique" composites may be useful in defining stocks. The great composite diversity displayed in the samples of Atlantic herring most probably reflects the very large population sizes involved.

In the absence of gene flow among spawning populations, we would expect a unique composite to be found in the same population as its most probable precursor. In three out of seven instances, precursors of unique composites occurred in different spawning populations (this result holds for all other equally parsimonious networks). For example, composite 9, which only occurs in the St. Lawrence sample, is the immediate ancestor of composite 20 from Trinity Ledge. In addition, the two unique composites which were maximally divergent (12 steps) occurred in the same population (Trinity Ledge 1985). These considerations, as well as the absence of any consistent geographic pattern of unique composites are consistent with the idea of gene flow.

Evidence for the ability of mtDNA analysis to detect subtle population differentiation is compelling (Avise et al. 1979; Lansman et al. 1981; Wilson et al. 1985; Bermingham and Avise 1986). However, since differentiation of mtDNA restriction patterns is a time dependent process (Kessler and Avise 1985), it is possible that there has been insufficient time to accumulate population specific differences in Atlantic herring (Grant 1984, 1985). Atlantic herring stocks, as they currently exist, can not predate the origin of the Gulf of Maine following glacial withdrawal 18,000 years ago (Kellogg 1980). In addition, since the effective population sizes of Atlantic herring stocks are very large, they would be expected to diverge only very slowly by lineage sorting (Neigel and Avise 1986).

Consistent, significant genetic differences among spawning groups of Atlantic herring is a sufficient, but not a necessary, condition to regard populations as discrete stocks. Our results do not support the hypothesis that discrete Atlantic herring stocks exist throughout the Gulf of Maine; however, the absence of such differences does not allow us to rigorously conclude that there is gene flow among the populations in question. More comprehensive sampling of mtDNA composites within and among populations in the western North Atlantic may better allow resolution of this problem. Regardless, for the sake of preserving variability, resources like the Atlantic herring should be managed under the assumption that every spawning group is a semi-discrete genetic entity.

ACKNOWLEDGMENTS

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POPULATION AND FISHERY CHARACTERISTICS OF ATLANTIC MENHADEN, *BREVOORTIA TYRANNUS*

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ABSTRACT

A stock assessment analysis of the Atlantic menhaden, *Brevoortia tyrannus*, fishery was conducted with purse seine landings data from 1940 to 1981 and port sampling data from 1955 to 1981. Virtual population (cohort) analysis was used to estimate historical stock sizes, rates of fishing, and numbers of recruits. The population exploitation rate (age 1 and older) ranged from 0.29 to 0.51 and averaged about 0.38 for the 1955-79 period. Recruitment at age 0.5 during the 1955-79 period ranged from 1.5 to 18.6 billion fish, with a mean of 5.1 billion. Classical spawner-recruitment relationships describe the data poorly. Growth and mortality data were used to examine yield per recruit for temporal and geographic fishing areas and for the entire fishery. Size at age data, while supporting an earlier hypothesis of density-dependent growth, show a trend toward slower apparent growth in the 1970's than is explained by this hypothesis alone. Yield per recruit of Atlantic menhaden dropped from 107 g for the 1970-72 period to 57 g for the 1976-78 period. A Graham-Schaefer production model estimate of maximum sustainable yield (MSY) for the 1955-79 period was 414,000 metric tons. A modified Pella-Tomlinson production model provided a MSY estimate of 557,000 metric tons. The latter estimate is probably unattainable given current temporal and geographic fishing patterns. Results of these analyses indicate that the Atlantic menhaden fishery suffers from growth overfishing.

Some fishing activity has been conducted on Atlantic menhaden, *Brevoortia tyrannus*, since colonial times, but the purse seine fishery and factory reduction activities began in New England about 1850 (Reintjes 1969). The geographic range of the modern reduction fishery was established by the 1930's (Nicholson 1971a) and the fishery underwent substantial expansion following World War II. Good discussions of the actual fishing operations and types of gear involved are contained in Reintjes (1969) and Nicholson (1971a).

With the exception of the 1950 fishing season, the Atlantic menhaden fishery has dominated total U.S. fishery landings in volume since 1946, when the Pacific sardine, *Sardinops sagax*, fishery was declining. This dominance continued until 1963, when, during its own decline, Atlantic menhaden landings were surpassed by the gulf menhaden, *Brevoortia patronus*, purse seine fishery. Gulf menhaden landings have dominated U.S. fishery landings since, and Atlantic menhaden currently account for about one-third of the total menhaden landings.

The U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries[3] began biological investigations on Atlantic menhaden in 1952. Studies were initiated during what were, in retrospect, peak landing years with the goal to determine the nature of population fluctuations and variability in geographic abundance (June and Reintjes 1959). Following the marked reduction in stock abundance that occurred in the late 1960's, studies were initiated to determine probable causes for the decline and to develop management options to avert a second decline.

The fishery for this migratory clupeid takes place primarily within states' jurisdictional waters (<3 miles from shore), and managerial authority rests with the individual states. Coastwide management plans are cooperatively formulated under the auspices of the Atlantic States Marine Fisheries Commission (ASMFC), but the implementation requires separate legislative or regulatory action by each member state. Individual states are not obligated to act upon cooperatively derived plans or management actions from the ASMFC.

Stock assessment studies provide fundamental scientific information required to formulate coastwide management actions. An early evaluation of the stock status of Atlantic menhaden,

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covering the 1955-68 fishing seasons, was prepared by Henry (1971). Applying virtual population methods (number of fish alive that will be caught in the future (Ricker 1958)) to landings from 1955 to 1969, Schaaf and Huntsman (1972) conducted additional analyses of the population dynamics of this resource. Stock status was again examined with production models using adjusted effort and landings through 1973 (Schaaf 1975a). Population dynamics and potential yield of Atlantic menhaden were further examined by Schaaf (1979), using estimates of numbers landed through the 1976 season; he also employed cohort analysis with Pope's (1972) approximation and the Leslie matrix (after Leslie 1945). In response to a request from the State/Federal Fishery Management Program, Atlantic Menhaden Scientific and Statistical committee, a population dynamics subcommittee was formed (Federal, state, and industry membership). Their report (ASMFC[4]) contained an indepth stock assessment (conducted by the Southeast Fisheries Center (SEFC) Beaufort Laboratory, NMFS) based on landings data through the 1977 season, and was the basis for the Atlantic menhaden management plan adopted by the ASMFC (ASMFC 1981). A computer simulation model of the fishery was developed in an independent analysis and was based on the 1965 through 1978 seasons (Reish et al. 1985; Ruppert et al. 1985). The general concensus of the earlier studies (Henry 1971; Schaaf and Huntsman 1972; Schaaf 1979; ASMFC fn. 4) was that the Atlantic menhaden stock was being overexploited and concern was expressed regarding the reduced spawning stock and/or the high rate of harvest of immature fish.

The primary objective of this report is to evaluate the stock status of Atlantic menhaden through the 1981 season. The more recent 1970-78 fishing seasons are emphasized, notably in presentations of yield per recruit. Effort, landings, and biological sampling data from 1955 through 1981 are used to estimate historic population sizes, age-specific rates of fishing mortality, actual and potential fishery yield, and to examine the spawner-recruitment relationship.

The secondary objective is to determine what historical series of events led to recent conditions in the fishery. This objective can be reasonably met by examining the geographic patterns of harvesting rates and the relative amount of effort expended in each geographic area.

The final objective is to generate some information on the relative abundance and age structure of the menhaden stock during the earlier, presampling period of 1940-54. This is accomplished by comparing, with inferences, the geographic patterns of harvest and effort distribution from the time period with port sampling data (and thus estimates of age-specific exploitation rates) to the patterns of an earlier period when only landings and effort data are available.

OVERVIEW OF LIFE HISTORY AND STOCK STRUCTURE

Hypotheses of the seasonal distribution and migration patterns of adult menhaden were formulated from observations of fish schools (June and Reintjes 1959; Roithmayr 1963) and analysis of age-length distributions (Nicholson 1971b). These hypotheses were later supported by results of tagging studies (Dryfoos et al. 1973; Nicholson 1978). Much of the population is believed to overwinter south of Cape Hatteras to northern Florida, and in late winter begins moving north. By summer, adult menhaden are normally found in dense schools in open coastal waters, bays, and sounds from northern Florida to Maine. These fish schools are stratified by age and size, with the average length and weight increasing with increasing latitude. In September, the most northerly portion of the population begins a southerly movement. During November, most of the adult population that summered in waters north of Chesapeake Bay move south around Cape Hatteras. These larger fish are followed in early December by a southward migration of young of the year that have emigrated from estuarine systems north of Cape Hatteras.

Atlantic menhaden spawning occurs to some degree during virtually the entire year, but not over the entire range at any given time. Evidence for this comes from an ovarian maturation study (Higham and Nicholson 1964) and observed distributions of menhaden eggs and larvae on the continental shelf (Reintjes 1969; Chapoton[5]; Kendall and Reintjes 1975; Judy and Lewis

[4]ASMFC (1980). Report of the Atlantic Menhaden Population Dynamics Subcommittee to the Atlantic Menhaden Scientific and Statistical Committee on the status of the Atlantic menhaden stock and fishery. Unpubl. Rep., 68 p. Atlantic States Marine Fisheries Commission, 1717 Massachusetts Ave., N.W., Washington, D.C. 20036.

[5]Chapoton, R. B. 1972. On the distribution of Atlantic menhaden eggs, larvae, and adults. Unpubl. manuscr., 76 p. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

1983). These authors inferred that menhaden spawn in waters north of Long Island from May to September, in the Middle Atlantic Bight south of Long Island from March through May and again in September and October, but primarily spawn in the South Atlantic Bight from October through March.

Menhaden are believed to spawn in neritic waters over most of the continental shelf, as well as in bays and sounds in the Long Island waters and northward (Reintjes and Pacheco 1966; Nelson et al. 1977; Ferraro 1980). Higham and Nicholson (1964) concluded that menhaden do not spawn inside Chesapeake Bay. The buoyant eggs normally hatch in about 2 days, and the larvae have absorbed their yolk sac in about 4 days at a length of about 5 mm (Kuntz and Radcliffe 1917). The larvae subsequently enter estuarine systems when they are 10-34 mm long (June and Chamberlin 1959; Reintjes and Pacheco 1966; Lewis and Mann 1971). The seasonality of larval immigration varies among geographical sites within years and also among years at the same site, owing at least, in part to environmental conditions. Immigration of larvae has been observed from November through April in the South Atlantic Bight, October to June in the Middle Atlantic and Chesapeake Bay areas, and May to October in waters of Long Island and northward (see Reintjes and Pacheco 1966 for literature summary; Lewis and Mann 1971).

Following entry into estuarine waters, larvae progress to lower salinity waters and are frequently found in high abundance in smaller tributary estuaries, where they metamorphose into juveniles at a length of about 34 mm (June and Chamberlin 1959; Wilkens and Lewis 1971; Lewis et al. 1972). Young of the year generally remain in estuaries until the fall when most migrate downstream to larger rivers, bays, sounds, and into the ocean. The range in length of juveniles in the fall has been observed from 40 to 185 mm (Kroger et al. 1974). After their estuarine emigration in the late fall and early winter, juvenile menhaden from New England to the northern portion of the South Atlantic Bight migrate southward in dense schools often very close to shore (surf zone) (Kroger et al. 1971; Kroger and Guthrie 1973).

There are debates whether the Atlantic menhaden population is composed of more than one stock (June 1958, 1965; Sutherland 1963; June and Nicholson 1964; Nicholson 1972, 1978; Epperly 1981). However, the apparently similar movement patterns make what potentially may be genetically different spawning groups inseparable in the fishery. Hence, the menhaden population is currently treated as one exploited and managerial stock.

FISHERY DATA BASE

Records of landings of Atlantic menhaden taken by purse seine and the level of effort expended (vessel weeks) have been collected and maintained back to 1940. Early summaries (through 1971) are available from Nicholson (1971a, 1975) and more recently (through 1984) from Smith et al. (in press) (Fig. 1).

Fishery landings have been sampled and numbers at age landed estimated since 1955. The basic sampling methodology used was described by June and Reintjes (1959), with some recent modifications of sample size (Chester 1984). The efficacy and statistical design of the sampling methods are treated in detail by Chester (1984). The aging technique is described by June and Roithmayr (1960). Estimates of numbers at age landed for the 1955-64 seasons are available by fishing area on an annual basis only and are summarized by Nicholson (1975). Estimates of numbers at age landed used in this report for the 1965-81 seasons were available on a subseasonal basis (weekly) but varied slightly from some published annual summaries (Nicholson 1975 [through 1971]; Schaaf 1979 [through 1976]; and ASMFC 1981 [through 1980]) because of rounding differences, biostatistical error corrections, and use of a different estimation methodology[6]. Smith et al. (in press) gave landings at age values for 1965-84. Values we used were similar except that the 1970-81 values given in Smith et al. (in press) reflect minor corrections to the data file which were made subsequent to these analyses.

Size at age data were available from the port sampling data. Summaries of length and weight by age and geographic area are in Nicholson (1975) and more recently, Smith et al. (in press). Detailed treatment of seasonal length and age distributions by geographic area are contained in Nicholson (1971b, 1972).

[6]Some of the landing estimates (1965-1976) used in the development of ASMFC 1981 were obtained from an estimation procedure which used standardized, noncalendar weeks. While this procedure had some advantages relative to accuracy, it was not fully adaptable to the NMFS port sampling design. It was deemed more desirable to maintain a continuous set relative to estimation procedure. The differences are not large enough to alter analytical conclusions.

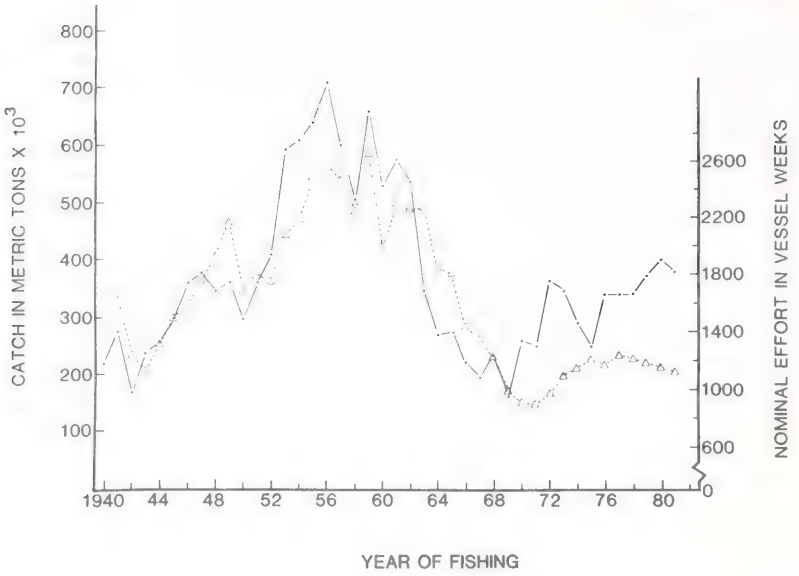

FIGURE 1.—Catch of Atlantic menhaden in thousands of metric tons from 1940 to 1981 (solid line) and fishing effort in vessel weeks from 1941 to 1981 (dashed line). Effort data from 1941 to 1968 are from Nicholson (1971a), catch and effort data from 1968 to 1981 are from Smith et al. (in press).

DESCRIPTION OF THE FISHERY

Geographic Fishing Areas

For purposes of summarization and analysis, June and Reintjes (1959) divided the U.S. Atlantic coast into four geographic fishing areas and one temporal fishing area (Fig. 2). With only a change in the boundary line between the south Atlantic and Chesapeake Bay areas (Nicholson 1975), these divisions have continued to be useful to date.

North Atlantic Area: Waters along the southern coast of Long Island, east of a line due south of Moriches Inlet, and waters northward.

Middle Atlantic Area: Waters west of a line running due south of Moriches Inlet (lat. 40°46′N, long. 72°44′W) on the southern coast of Long Island, southward to Great Machipongo Inlet, VA.

Chesapeake Bay Area: Chesapeake Bay proper and coastal waters south of Great Machipongo Inlet, VA (lat. 37°22′N, long. 75°43′W) to 36°20′N on the North Carolina coast.

South Atlantic Area: Coastal waters of North Carolina south of lat. 36°20′N to Cape Canaveral, FL.

North Carolina Fall Fishery: A temporal fishing area consisting of waters from Cape Hatteras south to the southern border of North Carolina, beginning some time between the last week of October and the second week of November, depending on the arrival of migratory menhaden from more northerly waters, to the end of February of the next calendar year (fishing usually stops by mid-January). For standardized data summary, the week of each season that ends between 8 and 14 November is taken to be the first week of the fall fishery.

Geographic Fishing Seasons

With the exception of state jurisdictional waters in the Chesapeake Bay area, the beginning and ending of seasonal fishing activities were determined by weather and the abundance of fish. Hence, the seasons were somewhat variable. Fishing normally began earlier and ended later in the year in the south Atlantic area, with progressively later beginnings and earlier endings proceeding northward. The south Atlantic (summer) fishery usually began in late March or April and normally ceased in late October or early November. Fishing in waters adjacent to Chesapeake Bay usually began about mid-May and ceased in November, but it occasionally persisted to early December. In the middle Atlantic

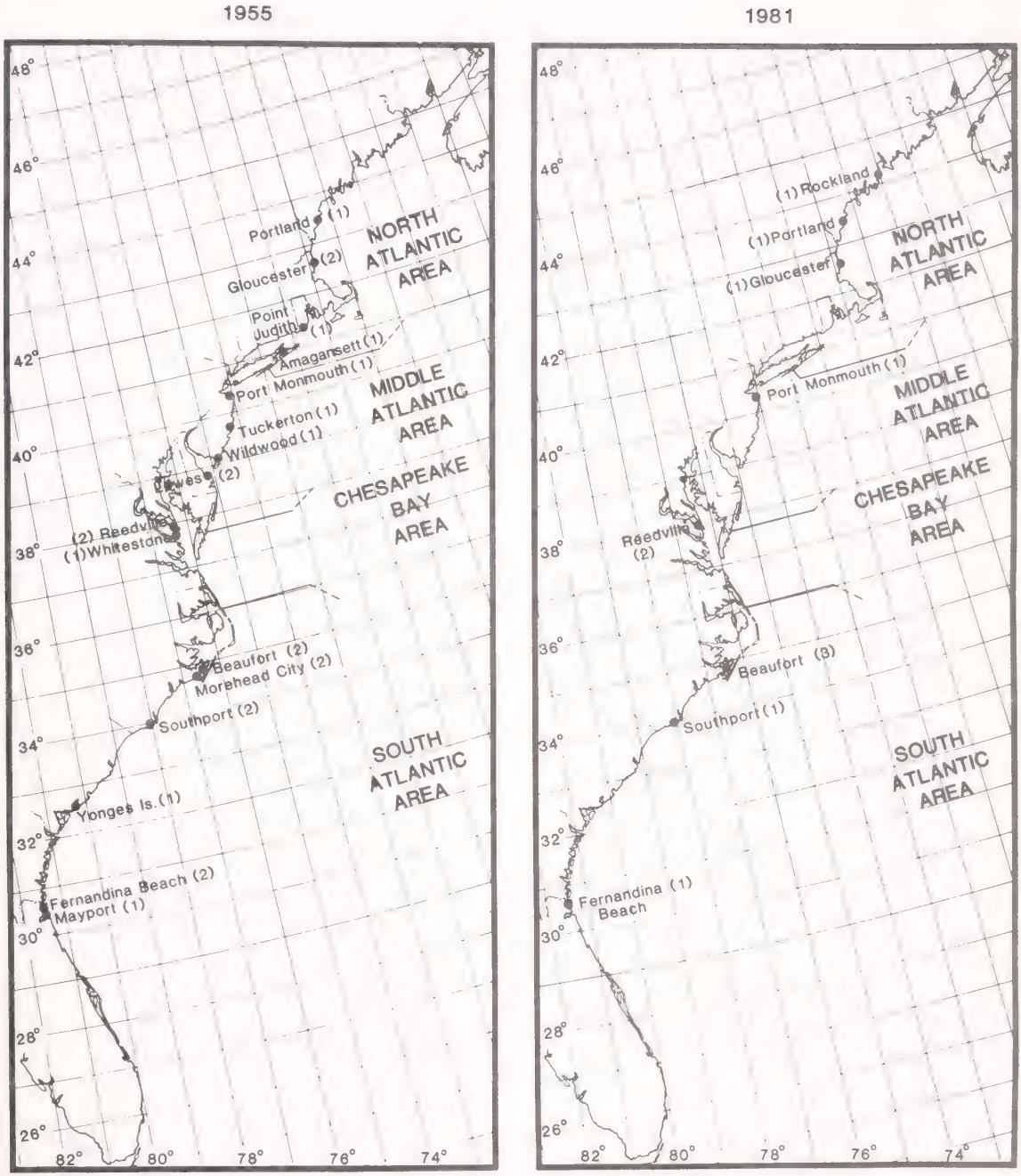

FIGURE 2.—Geographic fishing areas for the Atlantic menhaden purse seine fishery, and landing ports for 1955 and 1981 seasons. The number of plants operating at each port is given in parentheses.

area, fishing usually began about middle to late May and continued into late October. Fishing in the north Atlantic area usually commenced in late May to mid June and continued until mid-September or early October. Current state regulation opens the fishing season in Virginia waters of Chesapeake Bay on the third Monday in May and closes the season on the third Friday in November. All territorial waters of Maryland are closed to purse seine fishing the entire year.

Location and Number of Reduction Plants and Number of Vessels in Purse Seine Fishery

During 1955, 23 plants operated at 16 ports along the U.S. Atlantic coast from Maine to Florida. By 1981 this number had been reduced to 11 plants operating from 8 ports (Fig. 2). The number of vessels landing fish declined from 150 during the 1955 season to 64 by 1967 (Table 1). During 1981, 57 purse seine vessels landed menhaden.

TABLE 1.—Number of purse seine vessels that landed Atlantic menhaden during the fishing year by area, 1955-81 (from ASMFC 1981).

Year	North Atlantic[1]	Middle Atlantic	Chesapeake Bay[2]	South Atlantic[3]	Total[4]	Fall fishery
1955	39	48	20	34	150	51
1956	40	47	24	30	149	63
1957	33	46	25	31	144	64
1958	23	44	28	26	130	63
1959	34	45	31	25	144	59
1960	19	47	22	20	115	37
1961	21	47	23	20	117	44
1962	20	47	29	15	112	49
1963	10	46	36	16	112	46
1964	9	37	38	16	111	51
1965	6	13	38	19	84	46
1966	5	10	36	16	76	43
1967	0	4	32	16	64	46
1968	2	4	25	16	59	45
1969	3	4	22	16	51	36
1970	4	1	18	11	54	37
1971	5	2	20	11	51	32
1972	9	4	19	11	51	5
1973	10	6	23	11	58	4
1974	12	6	22	12	63	12
1975	9	5	22	14	61	17
1976	12	4	21	12	62	13
1977	12	5	24	10	64	16
1978	13	5	22	11	53	18
1979	11	4	22	13	54	18
1980	5	6	24	12	51	19
1981	8	7	23	13	57	19

[1]Vessels fishing from New England ports in recent years are all trawlers that convert to purse seine in summer. Some fish regularly and others sporadically
[2]Vessels that fished only in regular season. Does not include vessels added in October and November
[3]Includes only vessels that landed regularly in the summer fishery.
[4]Includes all vessels that landed fish during the year.

Trends in Nominal Effort, Landings, and Age Composition

Since the early 1940's, the Atlantic menhaden fishery has displayed a somewhat classical harvest pattern with an historic increase to a record high, fluctuations, decline, and a secondary slower regrowth (Fig. 1). After an initial slight decline, landings of Atlantic menhaden steadily increased from 167,200 t in 1942 through 1947. Nominal effort generally paralleled landings, but slightly lagged, from a low in 1943 to a minor peak in 1951 and rose to the record high of 712,100 t in 1956. Effort levels increased again in 1953 and reached a secondary peak in 1956 as well. Effort reached its highest level in 1959 with landings at their second highest level of 659,100 t. Landings dropped precipitously from 1962 to a record low 161,600 t in 1969, while effort dropped from 1964 and bottomed in 1971. Although fluctuating, landings showed a net increase from 1970 through 1981. Effort slowly increased up to 1977 and then began a declining trend.

All of the five fishing areas showed a net increase in catches from the 1940's to the peak year in 1956 (Fig. 3). But, the increase was disproportionately distributed between fishing areas. The middle Atlantic area showed the greatest relative increase, followed by the north Atlantic and Chesapeake Bay areas, with the south Atlantic and North Carolina fall fishery only showing slight increases (Fig. 4). While 1956 represented the year of peak landings for the fishery, only the middle Atlantic catches peaked during this year.

The increase in fishing effort expended during the 1940's to the mid-1950's was also disproportionately distributed between fishing areas, with the middle Atlantic showing the greatest increase, followed by the north Atlantic (Fig. 5). The Chesapeake Bay area showed a slight increase, while the south Atlantic and North Carolina fall fishery areas showed little, if any, actual increase in nominal effort.

Following 1956, the proportion of the catch taken in the middle Atlantic area decreased relative to the proportion of effort expended in that area. After 1962, effort (and catches) rapidly decreased in the middle Atlantic area, with both the effort and catches seemingly shifted to the Chesapeake Bay area (Figs. 4, 5). This was a relatively dramatic shift, considering that the middle Atlantic catch was generally dominated by age-2 and -3 fish while Chesapeake Bay catches were dominated by ages 1 and 2. Additionally, middle Atlantic fish were generally larger for any given age than those from Chesapeake Bay. Catches and effort also decreased in the north Atlantic area during the same time frame.

The Atlantic menhaden stock probably had its strongest and broadest age structure in 1955 and 1956, which also represent the first years when port sampling covered the full geographic range

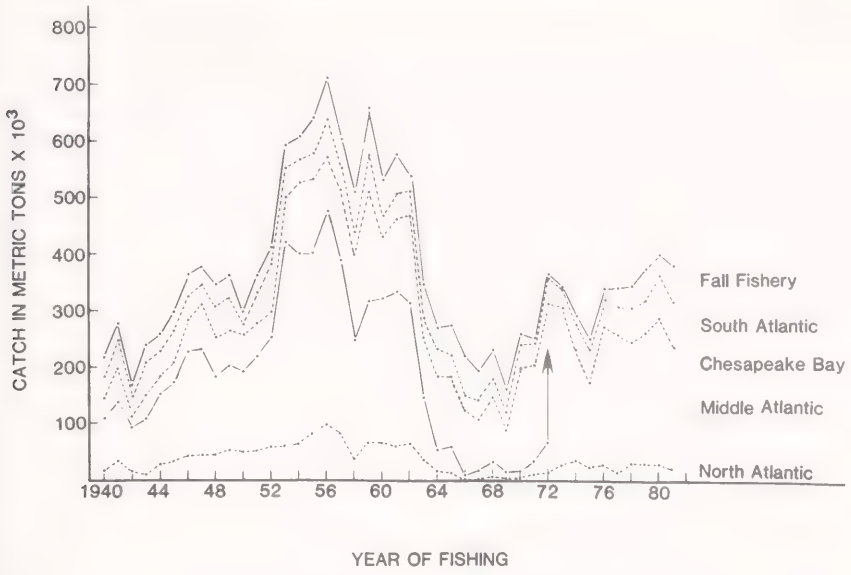

FIGURE 3.—Contribution to landings of Atlantic menhaden by fishing area and season in thousands of metric tons for years 1940-81. The middle Atlantic and Chesapeake Bay area landings are combined after 1972 due to confidentiality restrictions.

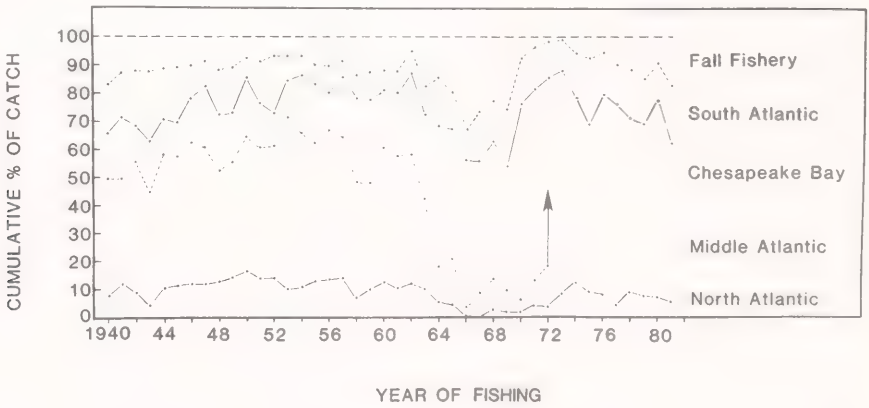

FIGURE 4.—Cumulative contribution by percent total landings of Atlantic menhaden by fishing area for years 1940-81. The middle Atlantic and Chesapeake Bay area values are combined after 1972 due to confidentiality restrictions.

of the fishery (Fig. 6). The number of older fish in the population was somewhat reduced by 1959, but showed a slight recovery in 1960. The age structure became markedly constricted by 1965, and drastically truncated by 1967. The age structure appeared to begin broadening slowly about 1972, and appears to be continuing this trend through 1981.

Although a few individuals aged 9 and 10 years were taken by the fishery during the late 1950's, the maximum age class with adequate representation for computational purposes is age 8. (Hence, the age category of 8+ is taken in this report to be age 8, which for most years contained only age-8 fish.) Individuals age 8+ were represented in landings from 1955 through 1966 fishing seasons. From 1967 through 1969 the oldest fish were age 6, and likewise; 1970 through 1974, 1976, and 1978, age 5; and again, 1975 and 1977, and 1978 through 1981, age 6.

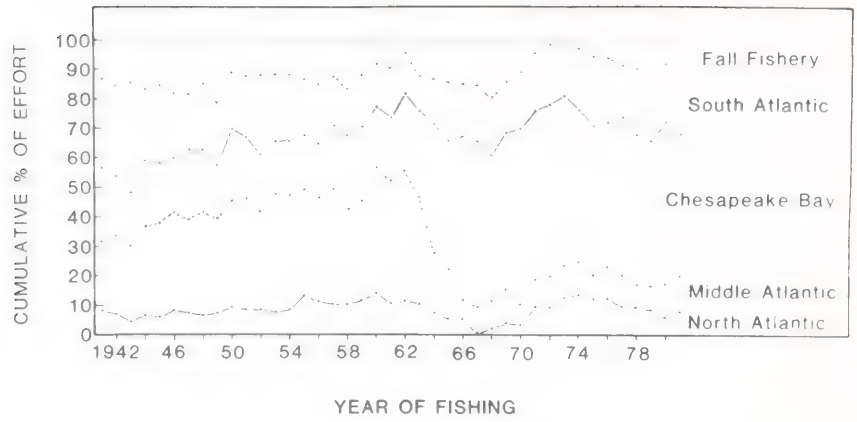

FIGURE 5.—Cumulative fishing effort on Atlantic menhaden as a percent of total, by fishing area for years 1941-81. (Data for 1941 through 1968 were adjusted (reduced) by Nicholson (1971a) to compensate for the small size of vessels that frequently fished in that area. The data for the middle Atlantic area were also adjusted, but to a lesser degree. Data from 1969 to 1981 are unadjusted. North Atlantic area data, adjusted by the Nicholson (1971a) criteria, would probably be less than half the amount shown, while the middle Atlantic area values may only be slightly reduced.)

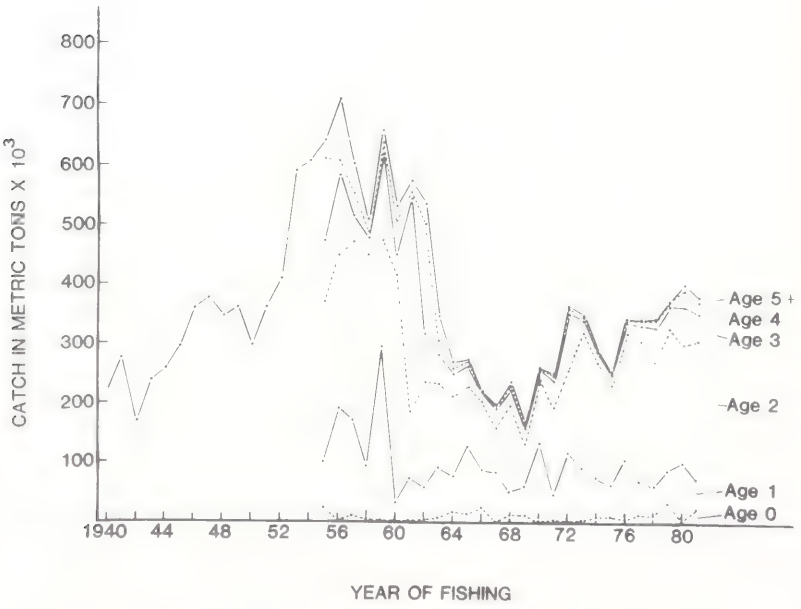

FIGURE 6.—Catch of Atlantic menhaden in thousands of metric tons by age group for 1955 to 1981.

SIZE AT AGE AND GROWTH ANALYSIS

It is necessary to derive two types of size at age and growth estimates because of the seasonal differential distribution of Atlantic menhaden by age and size (Nicholson 1972, 1978). Parameters are estimated by area to characterize the segments of the population normally harvested within that area and are estimated for the entire fishery to characterize the harvested population. Because relative harvest rates may vary among areas between seasons, apparent area-specific growth parameters are estimated for yield-per-

recruit analyses. On the other hand, parameters generated in each area are inappropriate (biased) for describing the entire population (or fishery). For example, growth rates and average size at age values for the north Atlantic area will be greater than those for the population, and similarly values estimated for the south Atlantic will be less than true population values. (The only exception is the North Carolina fall fishery, which apparently harvests a reasonably well-mixed migratory population.)

Size at age and growth estimates for the entire stock are needed for yield-per-recruit analysis for the entire fishery and to ascribe an average size at age for the spawning stock for each year. These estimates are obtained by appropriately weighting the sampling results from each fishing area, as will be shown.

Additionally, since growth of Atlantic menhaden has been shown to be inversely related to year class size (density-dependent) (ASMFC fn. 4), a condition predicated during the estuarine portion of the life cycle (Reish et al. 1985), growth equations must be computed for each year class. The fishing season is divided into quarterly increments for these analyses (Table 2). The analytical steps taken to obtain these size estimates and how they are used follows.

TABLE 2.—Quarterly time increments used in stock assessment analysis of Atlantic menhaden.

Quarter	Beginning week ending date	Ending week ending date
1	≥ 3/01	≤ 5/30
2	≥ 5/31	≤ 8/29
3	≥ 8/30	≤ 11/28
4	≥ 11/29	≤ 1[1]/4 29

[1]February of next calendar year, but same season.

Area-Specific Mean Size at Age and Growth Rates

Mean lengths at age by area by quarter for each of the 1965-81 seasons were estimated directly from the port sampling data as unweighted arithmetic means. These results were in turn arranged by specific year class and fitted to the von Bertalanffy growth equation using the computer package BGC3 (Abramson 1971). It was assumed that each mean length estimate was representative of the middle of the quarterly interval, i.e., for the first quarter (age X.0-X.25) the mean value is assigned to age X.125, etc. These fitted area-specific von Bertalanffy parameters were used to derive estimates of length at age for the beginning of each time interval. These estimates were in turn converted to estimates of weight at age for the area-specific yield-per-recruit analysis.

Mean Size at Age and Growth for the Entire Fishery

Predictive equations for growth which are representative of the population as a whole (entire fishery) are needed to estimate size at age for the spawning stock and for yield-per-recruit analysis of the entire fishery. For years 1965 to 1981, mean lengths at age by quarter for the entire fishery were obtained by weighting each area's estimate of mean length by its corresponding catch in numbers at age by quarter. Age 0.875 (fourth quarter age 0) was the youngest age for which mean length was calculated. These values were arranged by year class and were fitted to the von Bertalanffy growth equation.

Estimates of weighted mean length by quarter could not be calculated for the fish caught before 1965 because estimates of numbers at age landed by quarter by area were not available even though size at age is available weekly. Since much of the fourth quarter catch of the North Carolina fall fishery is composed of migratory stocks, it was presumed that a representative estimate of length at age for the entire population might be obtained from the fourth quarter values from this area alone. To test this hypothesis, mean lengths for the 1965 to 1978 year classes from the fourth quarter in the North Carolina fall fishery were fitted to the von Bertalanffy growth equation. The resultant curves were compared visually with results when all weighted mean length values were used. The results were quite similar when five or more data points were available and dissimilar to relative degrees when <5 data points were available. Because all year classes from 1955 to 1964 had at least 5 data points which met the above criteria, von Bertalanffy curves were fitted to these values (Table 3).

Weight-Length Relationship

The predictive growth equation used in this report uses length at age. Weight-length relationships were derived to estimate weight at age values. The greatest potential within year variation in weight-length parameters is expected among

TABLE 3.—Estimated von Bertalanffy growth parameters for Atlantic menhaden, year classes 1955-78.

Year class	L	K	t_0	n (means)	Age range (years)
1955[1]	339.49	0.5401	0.1234	7	0-7
1956	343.67	0.4598	0.0245	7	0-8
1957	324.49	0.6260	0.0707	7	0-7
1958	363.73	0.3637	−0.1163	7	0-7
1959	355.64	0.3631	−0.4709	6	0-6
1960	354.69	0.4009	−0.1481	5	0-5
1961	340.52	0.4514	−0.3506	5	0-5
1962	376.35	0.4012	−0.1122	5	0-5
1963	370.04	0.3494	−0.4652	6	0-6
1964	331.17	0.6138	0.0606	5	0-5
1965[2]	404.13	0.3187	−0.3529	17	0-6
1966	367.15	0.4575	−0.0645	18	0-6
1967	375.81	0.4539	0.1815	16	0-5
1968	415.22	0.2813	−0.7318	16	0-5
1969	356.19	0.5868	0.0530	18	0-6
1970	348.00	0.5351	0.0034	16	0-5
1971	356.82	0.4103	−0.2772	18	0-6
1972	316.74	0.6058	0.0767	17	0-5
1973	341.53	0.3884	−0.2947	20	0-5
1974	325.60	0.4329	−0.1280	22	0-6
1975	420.86	0.1779	−1.1445	21	0-6
1976	393.73	0.2410	−0.4372	20	0-5
1977	528.99	0.1455	−0.8354	16	0-4
1978	246.54	0.5807	−0.3399	12	0-3

[1]Year classes 1955-64 represented by fitted values for 4th quarter, area 5 (see text).
[2]Year classes 1965-78 represented by fitted values for weighted quarterly mean lengths

quarters. Because each area (except perhaps area 5) contains a limited portion of the range of sizes extant in the menhaden population, the weight-length relationship is estimated across areas, but within quarters. Annual variation was also assumed to exist, thus parameter estimates were calculated for each fishing season where subsequent yield-per-recruit analysis was intended (1970-78) using $\log_e$ transformed data and least squares regression (Table 4).

Annual Mean Weights Weighted by Catch

Estimates of annual weighted mean weight by age of Atlantic menhaden in purse seine catches were calculated to permit computations of age-specific and year class-specific biomass contributions to landings. Weighted mean weight for the entire fishery was calculated from the average weight by age by season for each of the five recognized areas of the fishery and then weighted by the estimated numbers caught by age in each respective area. These data were derived directly from the port sampling data and are not from von Bertalanffy derived lengths converted to weights.

VIRTUAL POPULATION ANALYSIS

Virtual population analyses (VPA's) were conducted to reconstruct population sizes and estimate rates of fishing mortality. Analyses were conducted on all age groups of the 1947-78 year classes which were represented in the 1955-81 landings. The backward sequential computations were performed using the computer program MURPHY written by Tomlinson (1970).

Instantaneous Rate of Natural Mortality

The estimate of the annual instantaneous rate of natural mortality (M) used in this report was 0.45. Early estimates were from catch statistics, 0.37 (Schaaf and Huntsman 1972); from preliminary tag-recovery analysis, 0.52 (Dryfoos et al. 1973); and from a more extensive tag-recovery analysis, 0.50 (mean of age-specific rates for ages 2 and 3) (Reish et al. 1985). The 0.45 value represents a mean of the range of available estimates. The implications of the selection of 0.45 for M are addressed.

Temporal Organization of Analyses

The time periods used in these analyses (Table 2) closely correspond to critical life history and fishery events. The birth date for a year class, and the beginning of a new fishing season for Atlantic menhaden, is 1 March. Because of the protracted spawning season of menhaden, young of the year may have been spawned as early as the previous August and as late as the following May or June, but most of the spawning takes place in the fall and winter (Nelson et al. 1977). The beginning of the fourth quarter (week beginning ≥ Nov. 29) is used as a finite date to estimate spawning stock size. Thus, the spawning stock in the fall (beginning of the fourth quarter) of the previous calendar year (age X.75) is defined to be the parental stock for a subsequent (1 March) year class. Recruitment is examined at age 0.5 (beginning of third quarter, age 0) and at age 1.0 (beginning of first quarter, age 1).

Three sets of VPA's were conducted with the length of the time intervals varied between sets. The first set provided the basic estimates for reconstruction of the historical population and the estimates of rates of fishing mortality. This series was done on an annual basis and involved all subject year classes. These estimates are used pri-

TABLE 4.—Weight-length regression parameters for Atlantic menhaden, by quarter and year, 1970-81 seasons ($\ln W = a + b \ln L$).

Fishing years	Quarter 1		Quarter 2		Quarter 3		Quarter 4		Annual	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
1970	−11.9324	3.1924	−11.5760	3.1224	−11.3909	3.0971	−11.5124	3.1087	−11.6666	3.1421
1971	−10.8692	2.9838	−11.0121	3.0135	−11.4336	3.0941	−12.0821	3.2044	−11.3620	3.0786
1972	−13.0384	3.3809	−11.5388	3.1072	−11.5989	3.1131	−11.5413	3.1028	−11.6553	3.1264
1973	—	—	−10.6360	2.9401	−10.7756	2.9741	−11.4291	3.0889	−10.9727	3.0060
1974	−12.8892	3.3503	−11.3321	3.0695	−11.2386	3.0552	−12.1803	3.2310	−11.4423	3.0896
1975	−10.3727	2.9027	−11.9798	3.1950	−11.7856	3.1555	−11.6995	3.1388	−11.8524	3.1703
1976	−10.9908	2.9972	−12.5123	3.2945	−12.4698	3.2933	−11.9663	3.1873	−12.3503	3.2642
1977	−12.6133	3.3110	−12.9689	3.3856	−11.9884	3.2043	−12.0643	3.2109	−12.5865	3.3137
1978	−12.3304	3.2666	−12.5737	3.3096	−12.0319	3.2124	−11.8477	3.1642	−12.3324	3.2653
1979	−11.9230	3.1950	−11.8170	3.1701	−12.0982	3.2243	−12.5516	3.2900	−12.4043	3.2793
1980	−12.2804	3.2580	−12.8763	3.3696	−11.9109	3.1884	−11.7750	3.1547	−12.3969	3.2792
1981	−12.2049	3.2386	−12.4031	3.2765	−12.6597	3.3215	−11.9663	3.1747	−12.5365	3.3004

marily in discussions of the impact of nominal effort and for modification of input variables for surplus production analysis.

The second series, with shorter time intervals, permitted a more precise apportioning of fishing mortality between fishing areas within a fishing season and provided within season estimates of numbers at age present in the population. This series was conducted on a quarterly basis and included the 1965-78 year classes. These estimates permitted a reconstruction of the fishery for the 1970-78 seasons which forms the basis of the subsequent yield-per-recruit analyses. The quarterly estimates of numbers at age are also used to estimate numbers of recruits for the 1965-78 year classes and the numbers of spawners that were ultimately derived from these year classes.

The third series was conducted to estimate numbers of recruits and their parental spawning stock for the 1955-64 fishing seasons. This series included the 1947-64 year classes and used mixed length time intervals. A 1/2-yr interval, which included ages 0.50 and 0.75 (quarters 3 and 4), was used to provide estimates of numbers of age-0.5 individuals present in the population. The time interval for age-1 fish was annual. Intervals for age-2 and older individuals were alternately three quarters of a year (quarters 1-3), corresponding to ages X.0-X.50, and one quarter of a year (quarter 4), corresponding to age X.75. This temporal construction of the numbers at age data required several adjustments which are discussed.

Additional VPA's were conducted to examine the sensitivity of results to the value of natural mortality used (0.45) and to the initial estimates of fishing mortality rates. A series of annual VPA's were conducted for the 1955-78 year classes with $M = 0.35$ and $M = 0.55$, which encompass the range of available estimates discussed earlier. Additional annual runs were conducted with varied starting F's for the 1955 year class, which for reasons discussed later, potentially represents a worst case situation relative to rates of convergence of estimates.

VPA Numbers at Age Landed Data Sets

The annual estimates of numbers at age caught were rearranged from a seasonal format to a year-class format. For the quarterly runs, the weekly catch at age estimates were summed to quarters and rearranged by year class. The mixed time interval VPA data sets were derived from the annual set, and thus required some approximations and adjustments to obtain a subyear format. Annual catches of age 0 (1955-64 seasons) were assumed to be in quarters 3 and 4 since the bulk of the age-0 catches occurred after 30 August (beginning of the third quarter). The major portion, if not all, of the catches of age-2+ fish (spawning ages) that were made during the fourth quarter time interval, was in the North Carolina fall fishery. During the 1965-69 fishing seasons, an average of 58% of the age-2+ fish that were landed in the fall fishery were landed during the fourth quarter. Hence, 58% of the fall fishery landings of age-2+ fish of the 1947-64 year classes were assumed to have been taken during the fourth quarter. The remainder of the total annual catch was assigned to the single three-quarter time interval (quarters 1-3). The time period used for the age-1 fish remained annual, so no adjustments were required.

Estimates of Initial Annual Rate of Instantaneous Fishing Mortality

Although a single method of estimation for the starting instantaneous annual fishing mortality rate (F) for backward calculations in VPA is desirable, a few year classes required alternate approaches. Year class-specific catch curves were examined visually. All years of age from the oldest to youngest that lie within a reasonably straight portion of a semilogarithmic catch plot were $\log_e$ transformed and regressed against age. The slope was taken as an estimate of $-Z$ (total instantaneous mortality) and by subtracting M a "general trend" F was obtained. Starting F's were obtained by this method for all year classes except 1947, 1948, 1949, 1954, 1966, 1971, 1974, and 1978. Since only 2 years of landings after full recruitment were available for the 1978 year class, an estimate of Z was made: $-\log_e$ (catch in numbers of age 3/catch in numbers of age 2). The estimate for 1949 was obtained similarly using ages 7 and 8. The 1954, 1966, 1971, and 1974 year classes experienced an apparently higher fishing rate during their last year in the fishery compared with that experienced 1 year earlier. Thus, starting F's were obtained from average VPA results from several other age classes caught in the same year. Starting F for age 8 of the 1954 year class was estimated as the mean F for ages 5-7 (year classes 1955-57) caught in the same 1962 season. Initial F for age 5 of the 1966 year class was the annual VPA estimate of age 4 from the 1967 year class. Similarly, starting values of F for the 1971 and 1974 year classes were the means of the same fishing season age-4 and age-5 values for the 1972 and 1973, and 1975 and 1976 year classes. Starting F's on age 8 for the 1947 (one age class represented) and 1948 (two age classes represented) year classes were means of similar fishing season VPA F's for ages 5-7. The initial annual F values and their sources for VPA are summarized in Table 5.

Conducting the VPA computations for the annual series was straight forward, as the trial F's were annual. The quarterly series and mixed time interval series required trial and error runs. Trial starting F's for these VPA's were adjusted downward until the sum of the F's within the last year (oldest fish of the year classes) were $\pm 0.5\%$ of the initial annual F estimate for each year class (Table 5).

Except for the sensitivity computations, the general results of the VPA's are presented and discussed where they are subsequently used. Using a relatively wide range of starting values for the 1955 year class, estimates of age-specific F and numbers at age present at the beginning of a season (Fig. 7) converged quite rapidly to similar values for the (younger) ages which dominate the fishery in both numbers and biomass (Figs. 8, 9). This is expected because of the relatively high rates of fishing mortality exerted on the stock (Ulltang 1977). The lower the exploitation rate, the slower the values will converge. The 1955 year class had the lowest starting F of any year class (Table 5) (other than 1947 which had only one age class represented) and relatively low to moderate rates of exploitation on all age classes. Thus the estimates for the other year classes should converge more rapidly than the one shown. Since it is highly unlikely that the initial estimates of F differ from true values to the extreme degrees tested, the VPA estimates used

TABLE 5.—Estimates of initial F for annual virtual population analyses (VPA's) of Atlantic menhaden, source of estimate, and ages involved, by year class.

Year class	Initial F	VPA's ages	Regression ages	Mean from VPA results[1]
1947	0.4862	8	—	yes
1948	1.3134	7-8	—	yes
1949	1.3498[1]	6-8	—	—
1950	1.6504	5-8	6-8	—
1951	0.9243	4-8	4-8	—
1952	0.8590	3-8	5-8	—
1953	0.8620	2-8	2-8	—
1954	1.1645	1-8	—	yes
1955	0.7006	0-8	2-8	—
1956	0.8557	0-8	2-8	—
1957	1.0651	0-8	5-8	—
1958	1.8497	0-8	4-8	—
1959	1.4325	0-7	3-7	—
1960	1.7620	0-6	2-6	—
1961	3.0108	0-6	4-6	—
1962	1.9074	0-6	2-6	—
1963	2.0482	0-6	2-6	—
1964	2.1116	0-5	2-5	—
1965	2.7386	0-5	3-5	—
1966	1.6194	0-5	—	yes
1967	1.1191	0-5	2-5	—
1968	1.6677	0-5	2-5	—
1969	1.9585	0-6	3-6	—
1970	2.2554	0-5	2-5	—
1971	1.5437	0-6	—	yes
1972	1.7143	0-5	2-5	—
1973	1.5403	0-5	2-5	—
1974	1.4321	0-6	—	yes
1975	1.3185	0-6	2-6	—
1976	1.0167	0-5	2-5	—
1977	1.3079	0-4	2-4	—
1978	1.4391	0-3	—	—

[1]See text

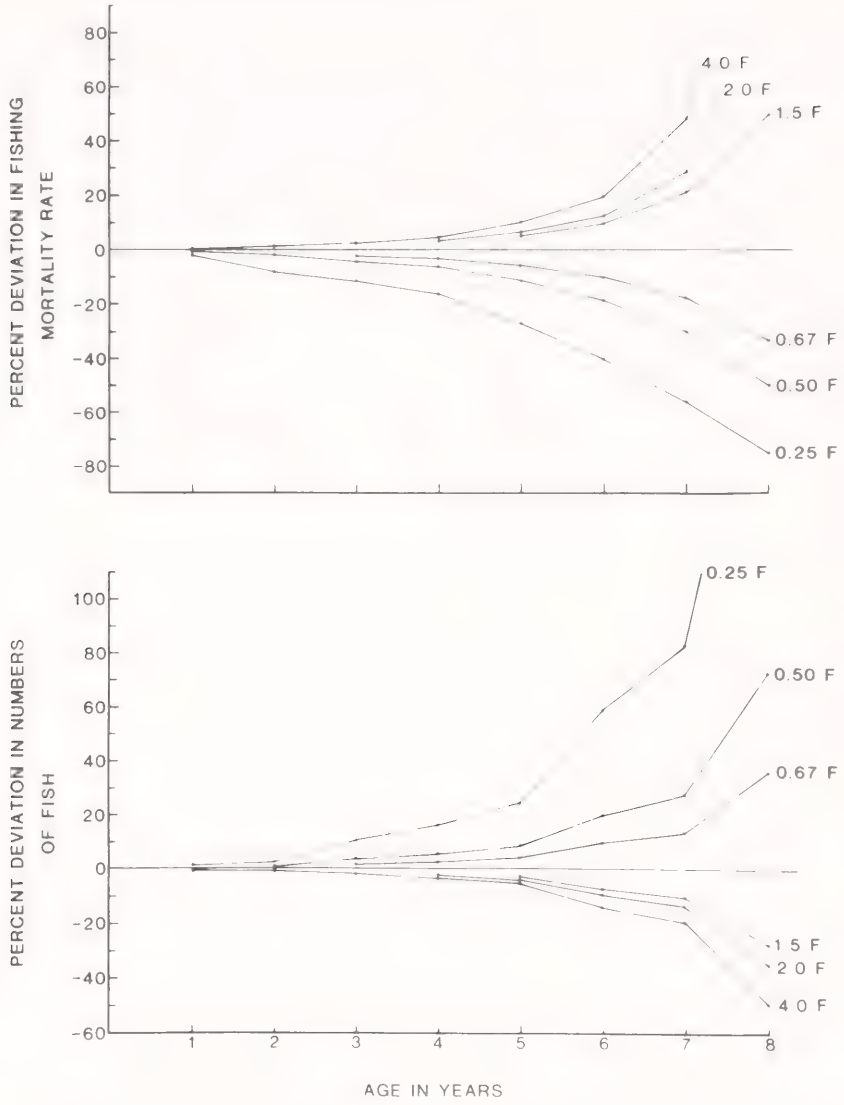

FIGURE 7.—Deviations in annual VPA (virtual population analysis) estimates of numbers at age present in the population and age specific fishing mortality rates for Atlantic menhaden resulting by varying the initial rate of annual F by the multiples shown. The estimates are for the 1955 year class (initial F = 0.7006).

here should be considered reasonably precise (and stable) relative to the initial F values.

Since F and M are additive with respect to Z, errors in these computations resulting from an incorrect selection of the rate of M are additive with respect to subsequent estimates of F, and estimates of numbers at age present in the population will differ in a proportional fashion. In other words, if our selection of the estimate of M is too great, numbers at age are overestimated, and if M is too low, the reverse is true (Fig. 10). Similarly, estimates of year class size vary by a nearly constant proportion (Fig. 11). The range of available estimates of M is relatively narrow, hence it is unlikely that conclusions reached in this report would be altered even if the estimate of M for these analyses were allowed to vary randomly within these bounds between years.

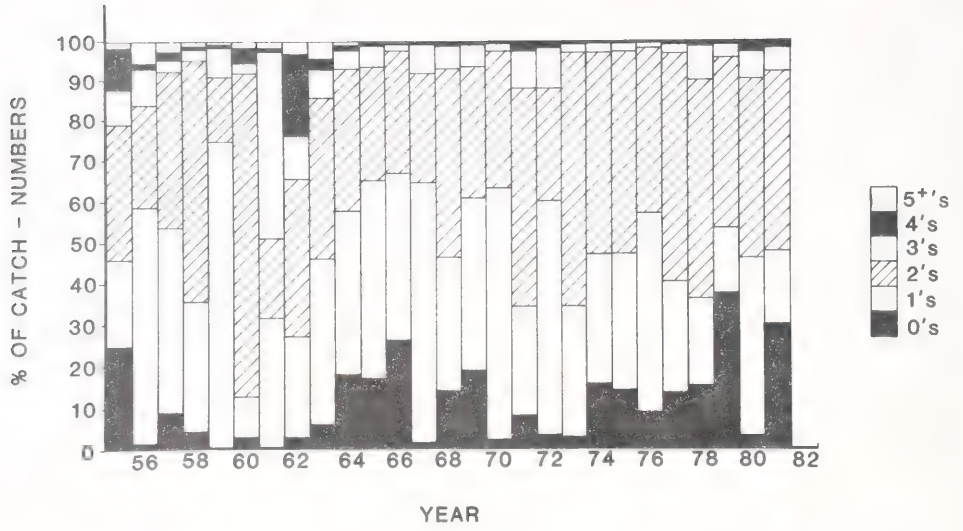

FIGURE 8.—Contribution in percent of total numbers of Atlantic menhaden landed by age group, from 1955 to 1981.

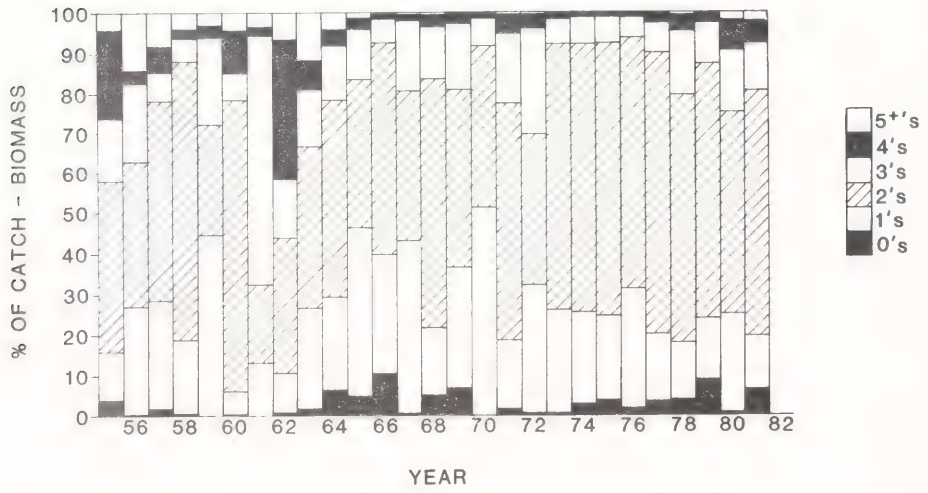

FIGURE 9.—Contribution in percent of total biomass of Atlantic menhaden landed by age group, from 1955 to 1981.

SPAWNER-RECRUITMENT RELATIONSHIP

Estimates of Numbers of Spawners

Higham and Nicholson (1964) concluded that a few age-1 Atlantic menhaden and most age-2 fish are sexually mature by the end of the season. The simplifying assumption for purposes of estimating spawning stock in these analyses is that no age-1 fish and all age-2 fish are mature by the beginning of the fourth quarter. This assumption was also used in other studies (Nelson et al. 1977; ASMFC fn. 4; Schaaf and Huntsman 1972).

Estimates of the number of fish age 2.75 and greater alive at the beginning of the fourth quarter of any given year n comprised the parental spawning stock for year class $n + 1$. The estimates of number of spawners resulting from the 1947-64 year classes were obtained from the mixed time-interval VPA series. The number of spawners from the 1965-78 year classes were ob-

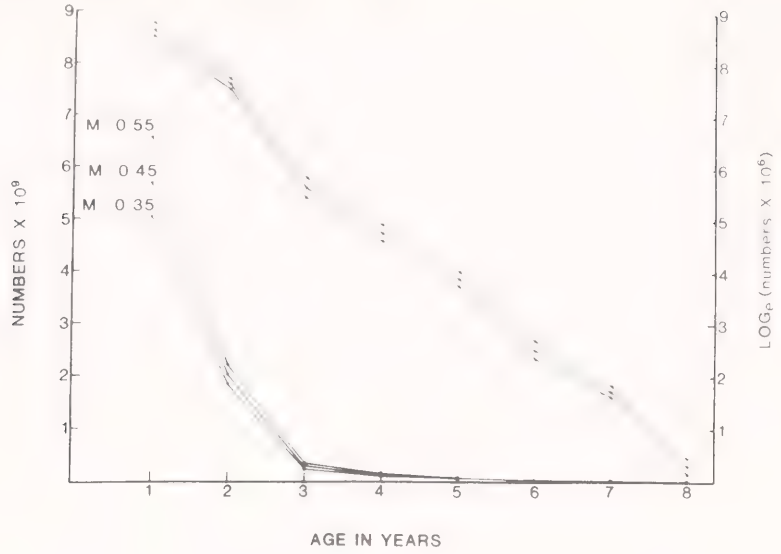

FIGURE 10.—VPA (virtual population analysis) estimates of numbers at age present in the Atlantic menhaden population for the 1955 year class for three levels of natural mortality (lower left), and natural logarithms of these same numbers at age (upper right).

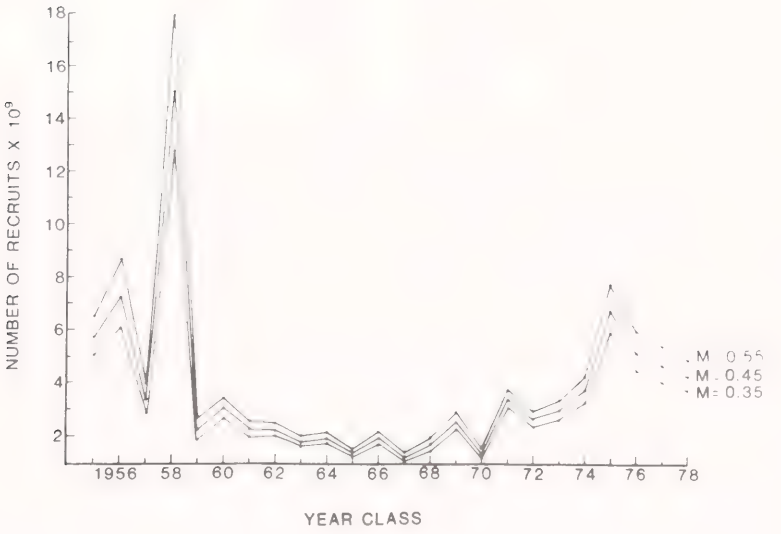

FIGURE 11.—Annual VPA (virtual population analysis) estimates of numbers of Atlantic menhaden recruits at age 1 for three levels of natural mortality.

tained from the quarterly VPA series. These estimates were rearranged to correspond to fishing seasons (Table 6). There were no estimates for numbers at age landed in the 1954 North Carolina fall fishery. Hence, the parental spawning stock for the 1955 year class was obtained by using 1955 estimates for age X.0 and back-calculating numbers at age to the beginning of the 1954 fourth quarter (age (X − 1).75) with mean fourth quarter survival rates at age for fishing years 1955-57. An additional adjustment was made to complete the estimates of spawning stock size. If an age group was represented during quarters 1-3 but not in quarter 4 of the last year it

TABLE 6.—Estimates of spawning stock size in thousands by age for Atlantic menhaden, 1954-81 seasons, at start of the fourth quarter of each fishing season.

	Age						
Year	2.75	3.75	4.75	5.75	6.75	7.75	8.75+
1954[1]	720,068.8	966,532.5	158,421.1	44,416.7	10,592.6	2,383.0	NE
1955	750,253.7	216,441.3	325,276.2	50,554.4	12,061.1	3,463.6	932.1
1956	285,976.8	213,151.0	102,272.1	98,950.9	11,254.9	2,541.6	593.9
1957	321,399.1	99,134.2	72,526.3	35,097.5	19,882.5	1,250.7	362.0
1958	1,060,499.7	145,248.4	46,161.4	29,036.6	11,021.2	5,504.1	82.2
1959	330,845.0	366,056.3	65,942.6	19,506.9	7,873.1	2,094.9	1,339.2
1960	2,662,230.0	144,140.8	125,048.6	20,387.2	5,552.2	1,337.9	693.7
1961	432,466.5	736,311.5	69,834.8	46,372.7	6,667.1	1,300.3	144.1
1962	215,894.3	84,439.3	97,991.5	18,987.4	6,579.9	1,795.1	258.7
1963	173,757.5	43,433.2	17,968.5	15,709.5	2,756.5	991.8	539.0
1964	151,149.8	26,764.3	4,358.7	2,199.5	1,112.9	157.6	194.2
1965	101,340.2	12,848.1	1,419.3	164.1	180.0	53.7	13.2
1966	194,222.2	18,780.6	1,401.8	15.5	18.0	27.4	5.4
1967	133,362.5	36,015.8	2,858.6	207.1	0.5	0	0
1968	122,033.7	16,235.3	1,227.0	199.0	8.1	0	0
1969	125,131.1	26,492.8	761.0	16.4	1.1	0	0
1970	175,837.2	34,303.4	6,017.2	48.1	0	0	0
1971	265,058.8	29,169.5	4,107.8	619.4	0	0	0
1972	64,386.9	14,863.7	1,187.3	766.8	0	0	0
1973	80,116.3	5,210.6	2,021.8	142.9	0	0	0
1974	94,348.3	7,760.3	241.5	153.0	0	0	0
1975	140,817.4	12,947.3	356.3	12.9	13.8	0	0
1976	212,735.5	37,466.2	2,306.5	164.1	0	0	0
1977	498,135.8	59,415.2	5,630.1	245.6	22.3	0	0
1978	451,889.2	80,962.9	13,390.0	927.6	0	0	0
1979	486,903.4	155,932.5	26,789.6	2,772.6	47.3	0	0
1980	424,606.5	103,707.0	42,254.5	4,995.9	909.8	0	0
1981	-No. est.-	57,691.0	14,868.6	7,335.7	397.5	0	0

[1]Derived from 1 March 1955 estimates (see text).

appeared in the fishery, it was assumed that some representatives were still present in the population at the beginning of quarter 4 (age X.75). Estimates of numbers present were obtained by a forward calculation using the mortality estimates of the previous interval obtained from the VPA's.

Estimates of Potential Egg Production

The age structure of the Atlantic menhaden population varied substantially during the time period under study. Therefore, an alternate method of examining spawning stock (i.e., potential egg production) as used by Nelson et al. (1977) was employed.

Sizes at age X.75 for spawners derived from the 1955-78 year classes were calculated from the von Bertalanffy growth parameters derived earlier for the entire fishery (Table 3). However, because of insufficient data, growth curves were not fitted to the 1947-54 year classes, so observed mean lengths at age during the fourth quarter were used for the spawners derived from these year classes. If the fourth quarter length at age was not available, means from the nearest three year classes were used.

Estimates of egg production were obtained from the expression used by Nelson et al. (1977), which was derived from data of Higham and Nicholson (1964):

$$\ln(E) = 0.3149 + 0.0176L$$

where, E = thousands of eggs produced per female, and
L = estimated fork length.

This equation was used with estimated mean length at age X.75 for fish 2 years and older. Assuming a 50/50 sex ratio, potential egg production by age by season was obtained by multiplying the values per female by number of females at age (Table 7).

Estimates of Numbers of Recruits

Estimates of the number of recruits for each year class were obtained from the results of the VPA's. The year class-size estimates for 1955-64 are from the mixed time-interval analyses and

TABLE 7.—Estimated number of recruits by year class at age 0.5 and 1.0, estimated number of spawners that produced the year class, and estimated egg production from the spawning stock, for Atlantic menhaden.

Year class	Number of recruits · 10^3		No. of spawners · 10^3	No. of eggs · 10^{12}
	Age 0.5	Age 1.0		
1955	7,888,342	5,621,258	1,902,414.7	219.659
1956	8,999,656	7,153,549	1,358,982.4	147.047
1957	4,419,989	3,263,196	714,741.2	83.977
1958	18,612,316	14,767,294	549,652.3	57.768
1959	2,722,999	2,164,428	1,297,553.6	143.822
1960	3,786,692	2,958,923	793,658.0	76.642
1961	2,769,147	2,210,534	2,959,390.4	156.058
1962	2,841,268	2,222,880	1,293,097.0	106.781
1963	2,304,564	1,754,140	425,946.2	37.508
1964	2,764,796	1,938,001	255,156.0	21.466
1965	2,072,852	1,430,539	185,937.0	13.806
1966	2,879,544	2,001,871	116,018.6	7.552
1967	1,522,438	1,209,954	214,470.9	17.017
1968	2,319,215	1,710,666	172,444.5	13.053
1969	3,448,326	2,611,940	139,703.1	11.240
1970	1,755,217	1,382,032	152,402.4	12.056
1971	4,513,962	3,539,073	216,205.9	17.594
1972	3,516,016	2,760,443	298,955.5	31.279
1973	3,908,494	3,085,954	81,204.7	8.044
1974	5,197,484	3,866,593	87,491.6	6.076
1975	9,024,340	6,932,136	102,503.1	6.591
1976	6,953,329	5,297,439	156,147.7	7.575
1977	6,619,024	4,827,413	252,672.3	11.966
1978	6,040,678	4,404,267	563,449.0	18.864
1979[1]	10,322,177	6,890,589	547,169.7	18.389
1980	NE	NE	672,445.4	26.045
1981	NE	NE	576,473.7	22.294

[1]Preliminary estimates.

those for 1965-78 are from the quarterly analyses. Estimates of recruitment were computed for both age 1.0 and age 0.5 (Table 7). Estimates at age 1.0 are provided for comparative purposes, as this age has been frequently used for studies on Atlantic menhaden (ASMFC fn. 4). Age 0.5 is used here to appropriately credit a year class with the numbers of juvenile fish removed from the population by the fishery during the fall and early winter. Although perhaps underestimates because the value of M (0.45) may be too low for fish younger than 1-yr old, these estimates are relatively consistent.

The degree of dependency of the number of recruits on the size of the parental stock has been examined by Schaaf and Huntsman (1972), Nelson et al. (1977), Schaaf (1979), and Reish et al. (1985). All earlier workers employed the Ricker (1954) model, but Reish et al. (1985) also used the Beverton and Holt model as well as the unnormalized gamma function. The published results indicate weak relationships, with substantial variability about both fitted models. Nelson et al. (1977) developed a multiple regression model to explain observed deviations from the Ricker model attributable to several annually varying environmental parameters, primarily Ekman transport, which would affect the oceanic larval stage.

The spawner-recruitment data (Table 7) were fitted with both the Ricker and Beverton-Holt models using a nonlinear least squares method (Marquardt's (1963) algorithm). Both models fit the data poorly (Fig. 12). The Beverton-Holt model is slightly better than the Ricker model if residual sum of squares is used as a goodness of fit criterion. The Beverton-Holt residual is only slightly less than that about a mean value, which assumes no relationship between numbers of spawners and numbers of recruits. Residual sum of squares in the Ricker model was slightly greater than results for the mean.

POTENTIAL AND ACTUAL YIELD

Production Models

The application of production models to the Atlantic menhaden purse seine fishery is hampered on theoretical grounds by two major conditions: 1) the fishery has not been operating under equilibrium conditions, and 2) fishing effort is not proportional to fishing mortality (F). The catchability coefficient (q) is inversely related to population size (Schaaf 1975b). Schaaf and Huntsman (1972) and Schaaf (1979) circumvented this latter problem by adjusting effort to a base year.

The effects of this problem were reduced in this analysis by using an estimate of population F for the independent variable instead of adjusting effort (Nelson and Ahrenholz 1986). To estimate a population rate of fishing mortality (F_{pop}), estimates of the population sizes (excluding 0-age fish) at the beginning of each fishing season from 1955 to 1979 were reconstructed from annual VPA estimates. These were in turn divided into the estimated catch in numbers (excluding age 0), to obtain an estimate of population rate of exploitation (U_{pop}). By trial and error, estimates of F_{pop} were obtained for each fishing season from $F_{pop} = U_{pop} Z/(1 - e^{-Z})$, assuming $M = 0.45$ (Table 8).

A Graham-Schaefer curve was fitted to the catch and population fishing mortality data by Marquardt's (1963) algorithm. This procedure produced an MSY (maximum sustainable yield) estimate of 414,000 t at $F_{pop} = 0.574$. Recent population fishing mortality values have been slightly above and below this value, and yield has

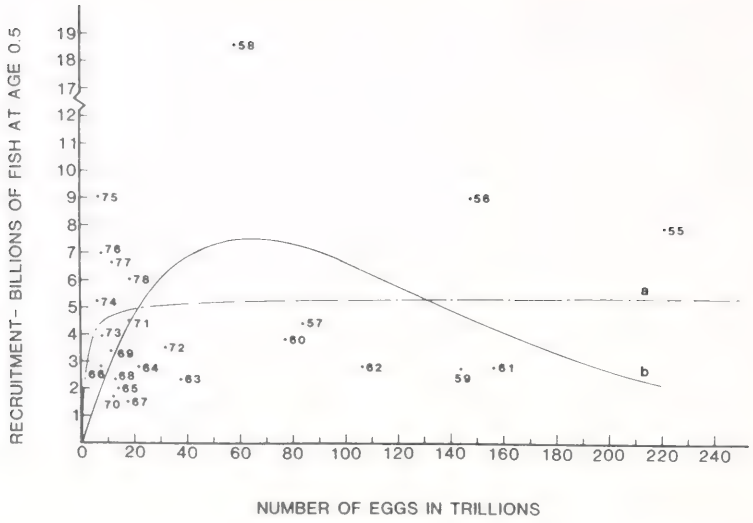

FIGURE 12.—Numbers of Atlantic menhaden recruits (R) in millions plotted against estimated egg production (P) in trillions for year classes 1955-1978. Curve a represents the fitted Beverton and Holt function, $R = 1/(0.00019 + 0.00027/P)$. Curve b represents the fitted Ricker function, $R = 325.35\ P \exp(-0.0158\ P)$.

TABLE 8.—Estimates of Atlantic menhaden population size and catch in numbers in thousands (age 1 to maximum observed age), population exploitation rates, population *F*, and catch in thousands of metric tons, by year.

Year	Population size	Catch in numbers	Population exploit. rate (*U*)	Population *F*	Catch (t)
1955	6,955,987.3	2,357,430.0	0.3389	0.532	641.4
1956	8,305,282.6	3,528,450.0	0.4248	0.721	712.1
1957	9,829,843.1	3,212,090.0	0.3268	0.508	602.8
1958	7,125,101.7	2,613,150.0	0.3668	0.590	510.0
1959	17,630,370.1	5,342,240.0	0.3030	0.462	659.1
1960	9,309,904.0	2,702,940.0	0.2903	0.438	529.8
1961	6,843,711.6	2,598,060.0	0.3796	0.618	575.9
1962	4,587,482.6	2,048,280.0	0.4465	0.774	537.7
1963	3,602,666.4	1,667,620.0	0.4629	0.816	346.9
1964	2,770,398.2	1,426,470.0	0.5149	0.961	269.2
1965	2,593,453.3	1,260,362.0	0.4860	0.878	273.4
1966	2,127,951.0	991,157.0	0.4658	0.824	219.6
1967	2,592,784.2	977,255.0	0.3769	0.612	193.5
1968	2,098,231.9	993,717.0	0.4736	0.845	234.8
1969	2,281,471.7	710,048.0	0.3112	0.478	161.6
1970	3,507,601.0	1,379,039.0	0.3932	0.648	259.4
1971	2,555,012.9	896,250.0	0.3508	0.556	250.3
1972	4,466,635.5	1,664,286.0	0.3726	0.602	365.9
1973	4,294,409.0	1,780,916.0	0.4147	0.697	346.9
1974	4,433,007.7	1,671,675.0	0.3771	0.612	292.2
1975	5,401,009.0	1,857,415.0	0.3439	0.542	250.2
1976	8,927,821.9	3,005,106.0	0.3366	0.527	340.5
1977	8,652,084.7	3,181,191.0	0.3677	0.592	341.2
1978	7,855,446.4	2,622,620.0	0.3339	0.522	344.1
1979	7,370,472.2	2,353,757.0	0.3193	0.493	375.7

remained slightly below the MSY value (Fig. 13).

Catch and F_{pop} values were also fitted to a modified version of the Pella-Tomlinson (1969) model, which compensates for nonequilibrium conditions (PRODFIT)(Fox 1975), assuming two significant year classes. This technique resulted in an MSY estimate of 557,000 t at $F_{pop} = 0.336$ (Fig. 13).

The scatter plot of yield/F_{pop} contains three

clusters of yield values: high abundance gears (1955-62), low abundance (high F_{pop}) years of 1963-68 (with the exception of 1967), and years of low to moderate population size (1969-79). These clusters are less distinct when yield is measured in numbers of fish rather than biomass. A Graham-Schaefer curve, fitted to fishing mortality and yield in numbers of fish, resulted in a numbers MSY of 2.383 billion fish at an optimum $F_{pop} = 0.522$ (Fig. 14). Each year's yield in numbers as compared to biomass (Fig. 13, 14) suggests that the fishery in the late 1970's was not produc-

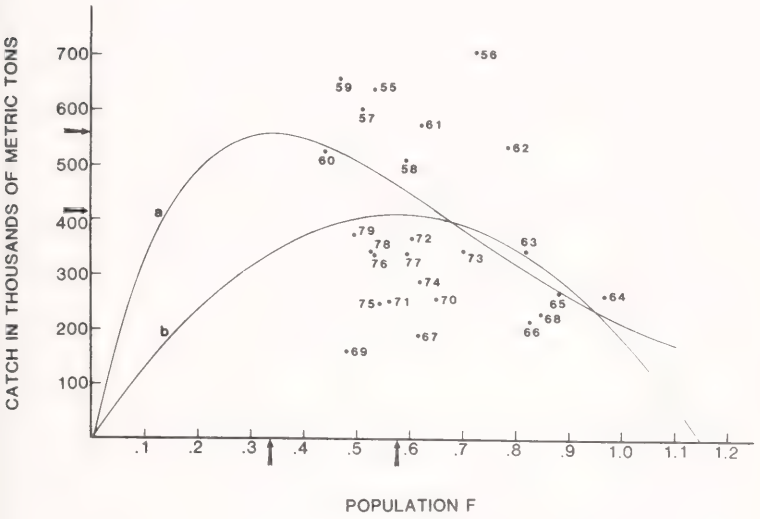

FIGURE 13.—Catch of Atlantic menhaden in thousands of metric tons plotted against estimates of population F for years 1955-79. Curve a is the result of fitting the Pella-Tomlinson's (1969) generalized yield function with adjustments for nonequilibrium conditions (PRODFIT, Fox (1975)). Curve b is a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

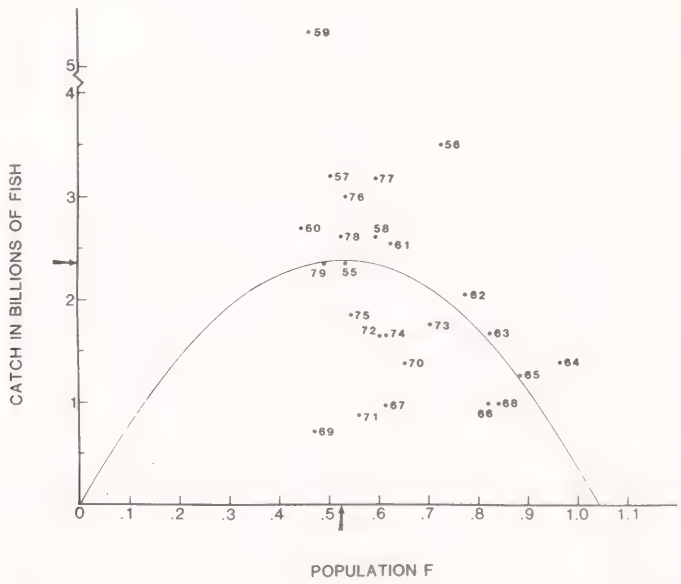

FIGURE 14.—Catch of Atlantic menhaden in billions of fish against estimates of population F for years 1955-79. The curve is the result of a nonlinear least squares fit of the parabolic (Graham-Schaefer) production model.

ing the biomass in landings in proportion to numbers of fish caught when compared to earlier years.

Catchability coefficients (q_{pop}) for the population were estimated directly by dividing the F_{pop} estimates by nominal effort (vessel weeks) for years 1955-79. A plot of these estimates on population size indicates a pronounced inverse relationship similar to that shown by Schaaf (1975b), who estimated q differently (Fig. 15). Additionally, there is a pronounced historical trend in the data. There appear to be at least two families of points and thus two functional curves in the figure, 1955-69 and 1970-79. Beginning in 1959, the catchability coefficient progressively increased, the stock size was decreasing, and the fleet was becoming more efficient due to modernization and increased vessel size, coupled with technological innovations in the fishery operations themselves. This trend in efficiency probably made the ascent from the earlier, lower q_{pop} series of years exceptionally rapid. As population size began to increase after 1971, the catchability coefficient reflected a steady decline in magnitude, but it was at a level almost twice as great (hence a doubling in killing power or efficiency[7]) as from the late 1950's and early 1960's. Therefore, the reduction in the number of vessels from 1955 to the present did not represent a proportional reduction in potential effective fishing effort. In spite of the compounding effect of a true increase in efficiency (fishing technology), q, and thus F for given levels of effort, appear to be responding in inverse fashion to population size.

The computed F_{pop} values are derived independently of nominal effort. Hence this set of values was used to determine if effort would be useful to verify trends in F at age or provide supportive information for improving the VPA estimates by employing more sophisticated models (see Deriso et al. 1985). A scatter diagram of the differences between estimates of F_{pop} and their mean on nominal effort demonstrated that no useful information is available from nominal effort when considering the entire time span involved (Fig. 16). The progressive increase in efficiency of the purse seine fleet, plus problems associated with estimating abundance with CPUE data from purse seine fisheries for schooling fishes (see Clark and Mangel 1979) makes nominal effort useful only for relatively short-time span comparisons between adjacent years, and then only when changes are pronounced.

Yield Per Recruit

Yield-per-recruit calculations for the 1970-78 fishing seasons were performed using the com-

[7]Given modern day work weeks, real time spent fishing, and intervessel competition, the killing power has probably more than doubled.

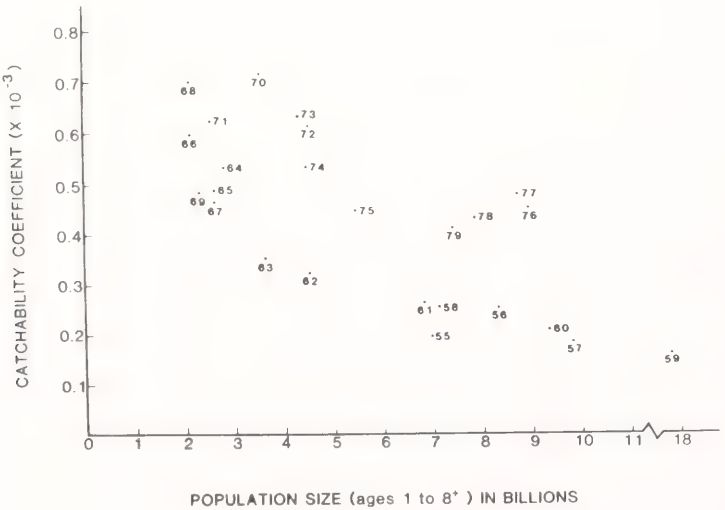

FIGURE 15.—Estimates of the Atlantic menhaden population catchability coefficient (q_{pop}) for years 1955-79, plotted against the estimated population size (excluding age-0 fish).

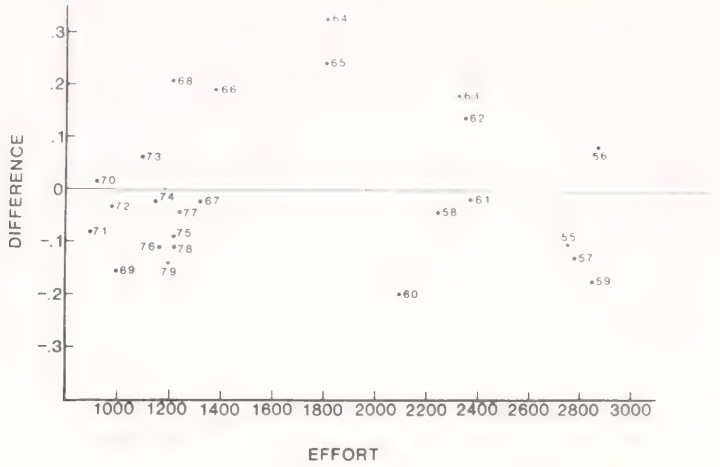

FIGURE 16.—Differences between observed Atlantic menhaden population fishing mortality rates (F_{pop}) and their mean plotted against nominal effort by fishing season.

puter program MAREA (Epperly et al. 1986) assuming exponential growth of the biomass in the population (Epperly and Nelson 1984). This program, modified for Atlantic menhaden from MGEAR (Lenarz et al. 1974), uses the Ricker-type yield-per-recruit model (Ricker 1975) and permits estimation of yield in each of the Atlantic menhaden fishing areas, with area-specific growth and fishing mortality rates. Each computer run of the model generates a matrix of yield per recruit at varied age of entry and multiples of F for each of the fishing areas (5) and one for the entire fishery. Yield for the entire fishery can be obtained either by summing yield from each area or by calculations based on input from the entire fishery estimated as a unit. A summation of the five matricies should be similar (but not equal) to the independently calculated entire fishery matrix. Input for the model includes estimates of area specific proportional fishing mortalities, estimates of weight at age by area and for the entire fishery, and an estimate of M (0.45).

Estimates of area-specific quarterly F at age were obtained by apportioning F at age for the entire fishery (obtained from the quarterly VPA, 1965-78 year classes) with the ratios of the number at age caught in a given area to the total number at age landed in the entire fishery. (The resulting proportional F's are not equivalent to true area specific F's, but are the correct values for the yield-per-recruit model used).

Area-specific length at age estimates for the beginning of each quarter for each year class were rearranged to correspond to fishing season, and converted to weight at age using season-specific weight-length equations (from Table 4). Parallel conversions were done on lengths at age for the entire fishery to estimate weights at age for the fishery as a whole.

Annual trends in historic yield per recruit were examined with the fishing mortality, age and size, and geographic pattern extant during each year from 1970 to 1978. Results from these computations indicate a severe decline in actual yield per recruit for the entire fishery and Chesapeake Bay area from 1971 to 1978 (Fig. 17).

Estimates of potential changes in yield per recruit under regimes of varied age at entry and (multiple) changes in fishing mortality rate were obtained by averaging parameters reflecting conditions during 3-yr intervals, i.e., 1970-72, 1973-75, and 1976-78 (Table 9). Attainment of the maximum potential yield from Atlantic menhaden in the purse seine fishery would have required a very high rate of fishing at a substantially delayed age at entry of about 3 years of age (Figs. 18, 19). More practically, yield could have been increased by reducing F's. For example, with a F multiplier of 0.6 and the current age of entry, the gain would have been 6.9% for the conditions of 1976-78 (Fig. 19, Table 9). With an increase in age of entry to 1.0 (eliminate the harvest of age-0 fish) the gain would have been 10.2%. The patterns of potential gain for conditions under the 1970-72 and 1973-75 time periods are similar, but of lesser magnitude (Fig. 18, Table 9).

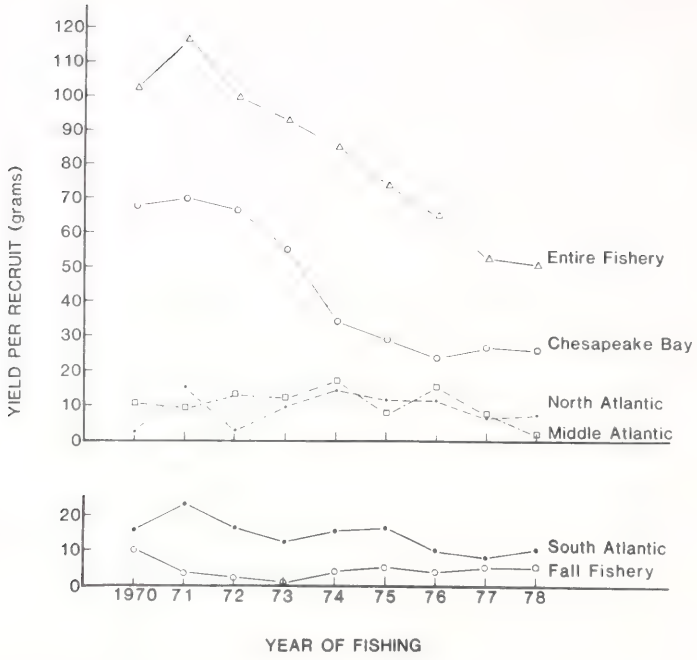

FIGURE 17.—Estimated yield per recruit of Atlantic menhaden for fishing patterns and growth prevalent during years 1970-78.

TABLE 9.—Estimates of percentage change in yield per recruit of Atlantic menhaden with varied age at entry and rates of *F* for 1970-72, 1973-75, and 1976-78. The *F* multiple of 1.0 represents the *F* at age vector extant during each of the three time periods.

Time period	Age at entry	*F* - multiple						
		0.4	0.6	0.8	1.0	1.2	1.4	1.6
1970-72	4.0	−35.8	−23.3	−16.1	−11.8	−9.2	−7.5	−6.3
	3.5	−21.9	−8.9	−1.7	2.6	5.3	7.3	8.7
	3.0	−12.7	0.2	6.2	9.8	12.0	13.4	14.4
	2.5	−4.6	6.8	12.1	14.9	16.5	17.5	18.1
	2.0	0.5	9.9	13.6	15.1	15.8	16.0	16.0
	1.5	−0.7	7.0	9.3	9.6	9.1	8.3	7.3
	1.0	−3.4	2.1	2.6	1.3	−0.6	−2.6	−4.7
	0.5	−3.9	1.4	1.5	(107.33)[1]	−2.1	−4.3	−6.5
1973-75	4.0	−7.7	4.6	10.5	13.6	15.4	16.5	17.3
	3.5	1.1	12.5	17.7	20.4	22.1	23.1	23.8
	3.0	10.5	20.2	24.2	26.2	27.3	27.9	28.4
	2.5	13.3	19.4	20.9	21.1	20.8	20.4	19.9
	2.0	12.8	15.2	14.8	14.0	13.2	12.5	12.0
	1.5	10.3	11.2	9.6	7.8	6.0	4.5	3.1
	1.0	8.2	8.1	5.6	2.9	0.5	−1.7	−3.7
	0.5	6.9	6.2	3.1	(84.07)[1]	−2.9	−5.5	−7.9
1976-78	4.0	−5.9	12.7	23.5	30.0	34.1	36.8	38.8
	3.5	1.5	18.8	27.8	32.7	35.5	37.1	38.1
	3.0	9.8	25.6	33.2	37.0	39.0	40.0	40.7
	2.5	12.1	22.7	26.0	26.5	26.0	25.1	24.2
	2.0	11.7	17.8	18.2	17.0	15.6	14.3	13.2
	1.5	9.6	14.0	13.2	11.0	8.8	6.7	4.9
	1.0	7.2	10.2	8.3	5.2	2.1	−0.7	−3.2
	0.5	5.0	6.9	3.9	(56.84)[1]	−3.8	−7.2	−10.3

[1]Estimated yield per recruit in grams for conditions of the time period, which is the base value for calculation of percentage change

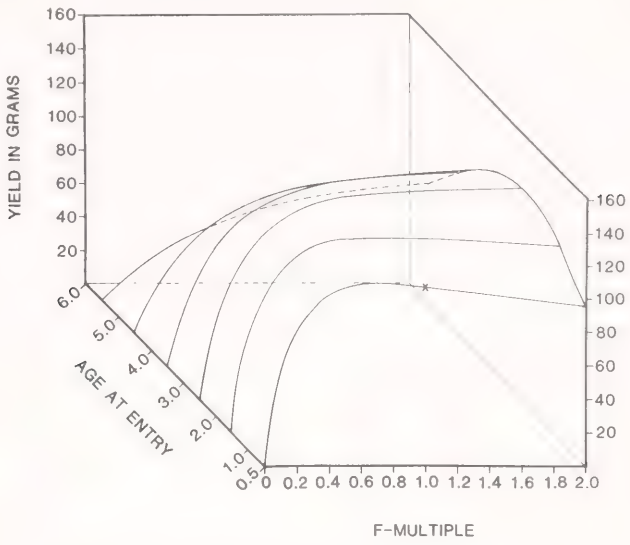

FIGURE 18.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for conditions extant during 1970-72. The X denotes estimate of actual yield per recruit for the time period.

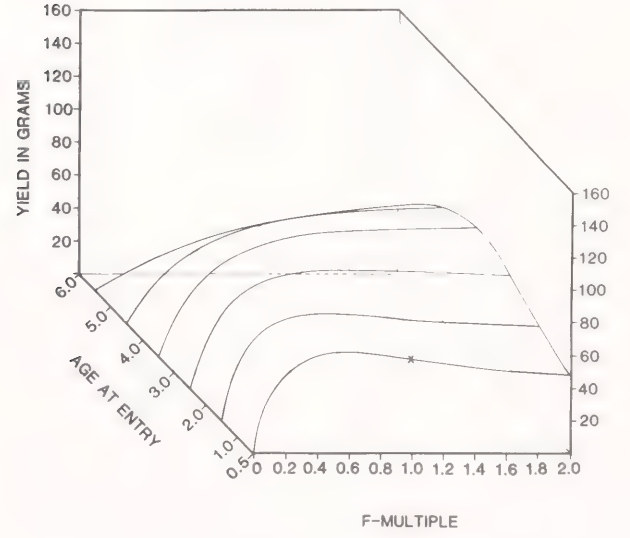

FIGURE 19.—Hypersurface representation of potential yield per recruit for Atlantic menhaden with varied age of recruitment and fishing mortality for fishing conditions extant during 1976-78. The X denotes estimate of actual yield per recruit for the time period.

Results from these analyses indicate a general reduction in the maximum potential as well as actual yield per recruit from the early to the late 1970's, but the maximum potential total yield is greater in the later time period due to increased numbers of recruits (Table 10). Thus, estimation of potential changes in yield by the Atlantic menhaden fishery from yield-per-recruit models becomes a function of density-dependent growth rates (lower yield per recruit with larger year

TABLE 10.—Estimates of yield per recruit (grams) and mean yield (thousands of metric tons) of Atlantic menhaden for three, 3-yr intervals, maximum possible yield per recruit (Y/R) and yield with the existing fishing pattern.

Years	Mean no. of recruits $\cdot 10^6$	Estimated Y/R (g)	Mean yield estimate (t)	Maximum Y/R (g)	Maximum yield (t)	Increase %
1970-72	2,711.8	107.33	291.1	127.56	345.9	18.8
1973-75	3,778.2	84.07	317.6	108.40	409.6	29.0
1976-78	6,340.5	56.84	360.4	80.49	510.3	41.6

classes), rate of fishing, geographical pattern of fishing, age of recruitment, and numbers of recruits.

The general conclusion reached with these analyses is that the stock suffers from growth overfishing. To determine if a different initial choice of a constant rate of M would alter this conclusion, the relative biomass of a hypothetical year class was estimated at specific ages with M equal to 0.35, 0.45, and 0.55 and F equal to zero. The growth equation for the 1970 year class (from Table 3) and the annual weight-length expression for 1972 (from Table 4) were used in these computations. The age of maximum biomass decreases with increasing rates of M, as expected, but even at $M = 0.55$ the age of maximum biomass exceeds 2.5 years (Fig. 20). This decrease (from about age 2.8 for $M = 0.45$) is insufficient to affect the conclusion of growth overfishing. However, if the initial choice of M is too high, the analyses are underestimating potential gains in total yield that could be realized by decreasing fishing pressure on younger ages. Similarly, if the choice of M is too low, the analyses are overestimating potential gains, but a net gain would still be realized within the range of available estimates of M.

Actual Yield by Year Class

Using the estimates of numbers caught by age and annual weighted mean weights at age, annual landings were apportioned into biomass at age landed and then summed by year class through age 5. The calculations provide estimates of yield by each year class. A plot of yield against year-class size reveals lower than expected yields from the 1975 and 1976 year classes, given their magnitude (Fig. 21). This trend appears to have started about 1973.

Comparisons of growth and mortality patterns were made of similar-sized year classes, 1955 and 1976, and 1956 and 1975, in search of causes of the observed decrease in yield. Differences in fishing mortality rates at age do not explicitly account for the dramatic differences in yield between the two pairs of similar-sized year classes (Table 11). The 1955 year class was harvested at a greater (less desirable) rate during the critical

FIGURE 20.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, exposed to three rates of natural mortality. If the year class was harvested instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

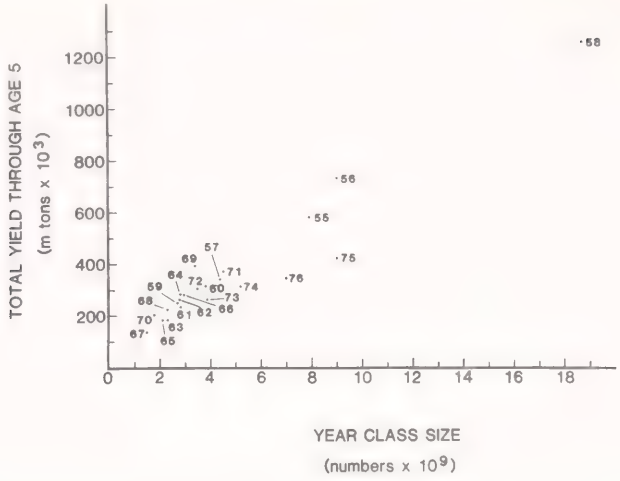

FIGURE 21.—Estimated yield contribution of Atlantic menhaden in thousands of metric tons, by the 1955-76 year classes through age 5, plotted against year class size.

TABLE 11.—Estimates of annual F at age for the 1955 and 1976, and 1956 and 1975 year classes of Atlantic menhaden, through age 5.

Year class	Age					
	0	1	2	3	4	5
1955	0.10	0.58	1.56	0.39	0.43	0.90
1976	0.04	0.27	1.51	0.57	1.04	1.02
1956	<0.01	0.32	0.88	0.74	0.61	0.48
1975	0.03	0.34	1.60	1.48	0.60	1.82

ages of 0-2 than was the 1976 year class. In fact, yield from the 1955 year class could have been markedly increased with a reduced fishing rate on these younger fish. The harvest rates of the 1956 and 1975 year classes were similar for ages 0-1, but markedly greater at age 2 for the 1975 cohort. While the high age-2 fishing mortality rate probably contributed to the lower yield, it did not fully explain the marked difference. The generally higher rates of F for ages 3-5 exhibited for both the 1975 and 1976 year classes were probably inconsequential for this comparison of yield.

While an increase in the true value of natural mortality could cause a decrease in total yield by year class, differences in growth provide a more obvious explanation for the differences within these two pairs of year classes. Growth curves (in length and weight) for the 1956 and 1975 year classes and the 1955 and 1976 year classes show that individuals were much smaller during the dominant harvest ages (1-3) for the two most recent year classes (Figs. 22, 23). These differences could be great enough to account for most of the differences observed in yield. Slower relative growth in post age-1 fish has been apparent for year classes 1973-78.

To determine if age of maximum theoretical biomass had changed owing to the different (flatter) shaped growth curves displayed by the year classes in the later 1970's, the relative biomass at age of an unfished hypothetical year class was estimated with the growth equation for the 1975 year class with M equal to 0.45 and the annual weight-length expression for 1972. The results display an increase in maximum age (to about 3.25 years), a decrease in total biomass, and a much slower ascent and even slower descent from maximum biomass than results for the 1970 year class growth curve (Fig. 24). These results indicate that age of entry to the fishery could have been greatly delayed in the later 1970's with little chance of losing yield.

Given the progressive decrease in average size at age of fish in the age classes which dominate landings (Fig. 25), the decline in yield per recruit following 1971 (Fig. 17) is expected. However, the rapid decline in size at age is not entirely ascribable to density-dependent growth. More importantly, the potential for increased yield with reductions in F is probably greater than the results from the MAREA yield-per-recruit model indicate owing to the likelihood of size selective fishing and the potential for differential stock-specific growth rates. Additionally, the relatively high MSY estimate obtained from the PRODFIT

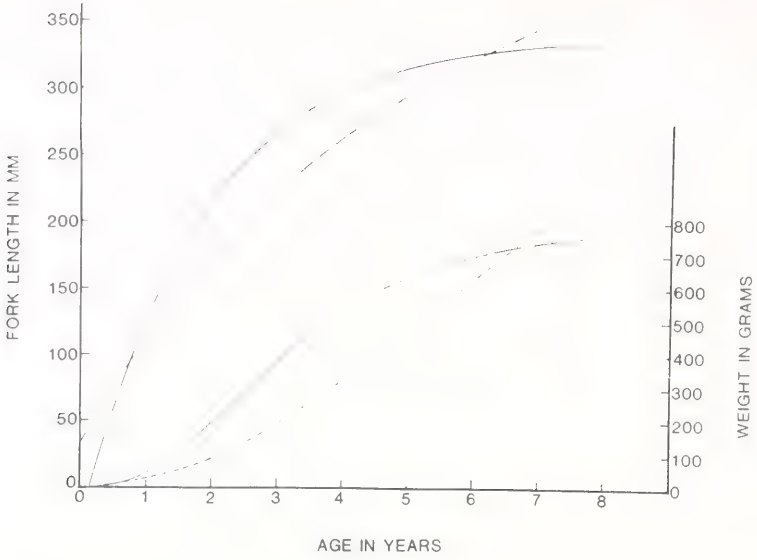

FIGURE 22.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1955 (solid curves) and 1976 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

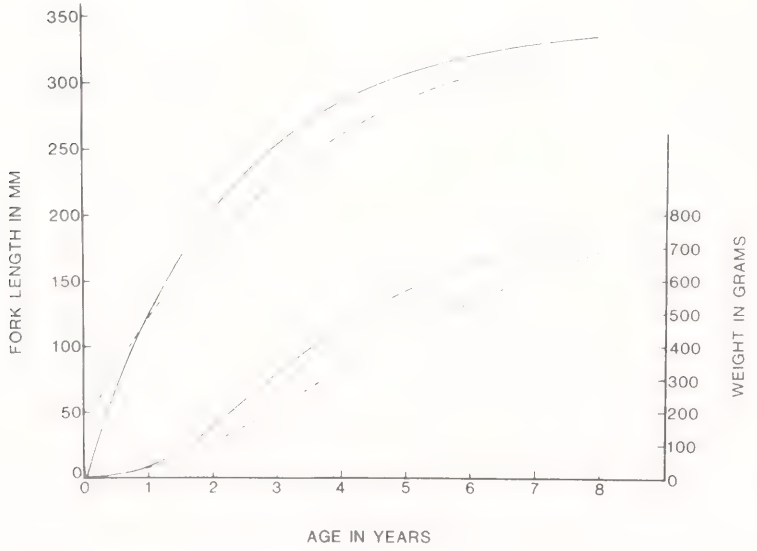

FIGURE 23.—Comparative fitted von Bertalanffy growth curves of two similar-sized (numbers of fish) Atlantic menhaden year classes, 1956 (solid curves) and 1975 (dashed curves). Upper curves are fork length in millimeters, and lower curves are weight in grams.

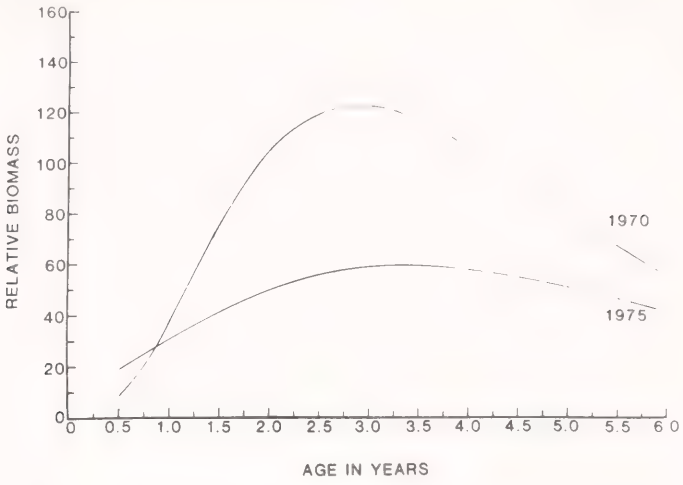

FIGURE 24.—Age-specific relative biomass estimates of a hypothetical year class of Atlantic menhaden in the absence of fishing, with growth parameters estimated for the 1970 and 1975 year classes. If harvesting occurred instantaneously at any given age, the corresponding ordinate value would represent yield per recruit in grams.

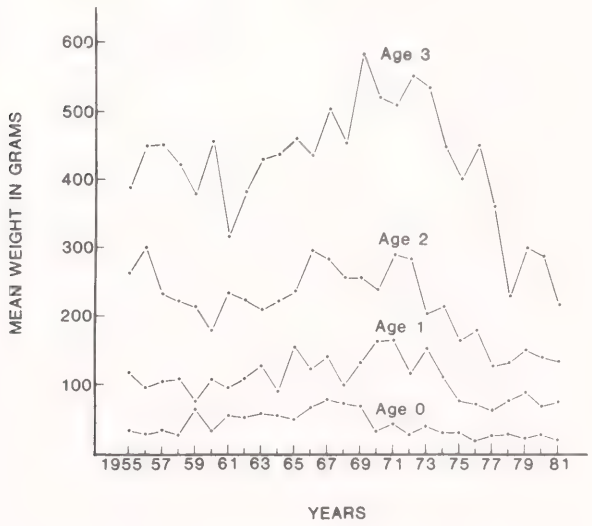

FIGURE 25.—Weighted mean annual weight of purse seine landed Atlantic menhaden, ages 0-3, for years 1955-81.

solution shown earlier may be more realistic than first impressions would indicate. However, to attain that level of harvest would require a restructuring of the fishery, and continued moderate to high levels of recruitment to sustain it.

GENERAL DISCUSSION

With estimates of year-class sizes, exploitation rates, and an understanding of the interaction of population size and effort relative to rates of fishing mortality, the trends observed in the fishery since 1955 are more readily explained. Additionally, this information permits inferences to be drawn about the earlier presampling period of the 1940's and early 1950's. The major premise of this discussion is that harvest levels and effort of the earlier presampling period were probably near

the maximum that the population could support, and thus the rather rapid growth of the fishery in the early to mid-1950's was a response to a substantial increase in abundance of Atlantic menhaden and not simply increased effort applied to an underexploited stock.

Changes in stock abundance due to fluctuations in spawning success were prevalent in the 1940's. This conclusion is drawn from the statement of purpose for study given by June and Reintjes (1959). They noted changes in abundance among geographic areas and seasons and some poor catches. This condition is expected when recruitment fluctuates in a fishery that has a stock which is differentially distributed by age and size.

Data from early years indicated a limited resource. Catch closely paralleled effort for the 1941-47 seasons, but catches during 1948 and 1949 (about 350,000 t) were less than expected given the effort expended (Fig. 1). Apparently the stock subsequently underwent a marked increase in abundance, noticeable first about 1952, but even more pronounced in 1953 and 1954. The fishery responded, as effort again began to rise, but lagged for the next two or three seasons. In 1959 catches were dominated by the 1958 year class, which continued to provide significant biomass to the fishery through 1962.

It appears that the 1950's marked a period with above average recruitment, and this was accentuated with the apparently very large 1951 year class, followed by the three relatively large year classes of 1953, 1955, and 1956, and finally the largest documented year class of 1958. Recruitment did not return to the level of the 1955 year class (the lesser of the three documented large year classes) until 1975. To obtain some idea of relative sizes, a reconstruction of these earlier year classes was made using arbitrary, but conservative values for F (F = 0.25 for age 1 and 0.50 for age 2+) (Table 12). Given the (older) larger sized fish which were taken during the peak landing years, these speculative year class estimates are less than or nearly equal to a size necessary to support the large catches of the mid-1950's (see Figure 14 and Table 7).

The age structure of the Atlantic menhaden population has undergone at least two periods of expansion and contraction since about 1950, and has shown signs of expanding again by 1980 (Fig. 6). Inferences on early age composition were derived primarily from the early 1952-54 sampling of the fishery in the middle Atlantic area (June and Reintjes 1959, their appendix table 2). Age-5 and older fish were 1.0%, 0.8%, and 1.1% by number in the samples from that area for 1952, 1953, and 1954 as compared to 1.8% and 2.9% for 1955 and 1956. The 1951 year class dominated the catch during this period, comprising 84.59% of the samples as age 1, 98.05% as age 2, and 59.02% as age 3 in the middle Atlantic area and 87.11% as age 3 in the newly sampled north Atlantic area. Hence, as noted earlier, the stock probably had its strongest age structure in 1955 and 1956, which were coincidentally the first years for which port sampling covered the full geographic range of the fishery. This strength was due to the increased population size, subsequent decrease in the catchability coefficient, and thus a reduced fishing mortality on most age groups. Higher rates of survival led to more individuals in the older age groups. The landings were sustained above 500,000 t in the mid-1950's by contributions of the 1955 and 1956 year classes, but these year classes were too small to prevent an increase in mortality because of increased effort and the number of older fish were reduced by 1959. The large 1958 year class aided the replenishment of the older age groups, by about 1960. Without another large year class,

TABLE 12.—Estimates from virtual population analyses (mixed time interval, see text) of number at age in thousands on 1 March for the 1950-59 year classes of Atlantic menhaden. Bracketed values represent estimates obtained from back calculations using arbitrary values of F (0.25 for age 1 and 0.50 for ages 2+).

	Year class									
Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959
1	[3,943,235]	[10,782,529]	[3,162,907]	[4,504,191]	3,040,558	5,621,258	7,153,549	3,263,196	14,767,294	2,164,428
2	[1,958,152]	[5,354,445]	[1,570,653]	2,236,715	1,410,646	1,976,767	3,306,709	1,412,179	6,627,079	1,158,337
3	[757,298]	[2,070,784]	607,436	642,482	240,748	274,476	893,865	275,897	2,357,641	361,743
4	[292,878]	800,857	189,410	169,952	80,038	119,036	270,347	116,411	602,146	71,280
5	113,268	281,543	86,255	53,482	37,304	48,835	92,494	59,258	75,460	11,589
6	43,677	63,025	23,309	21,243	14,284	12,269	35,962	14,698	8,894	1,616
7	5,980	11,726	7,639	3,717	2,765	5,618	4,883	1,629	901	161
[1]8	600	3,564	1,446	478	1,162	1,331	640	92	48	—

[1]This age group may contain a small number of age 9 or 10 individuals, see text

mortality apparently again increased, as the age structure became markedly constricted by 1965, and drastically truncated by 1967. Recruitment began to improve by 1971, culminating with relatively large year classes in 1975 and 1979. Mortality rates for some ages began to decline during the late 1970's, and the older age groups began to strengthen, consistent with the decline of the catchability coefficient with increased population size.

With respect to yield per recruit, there appears to be no recorded period of Atlantic menhaden fishing when an ideal harvesting regime existed in the purse seine fishery. Age-0 fish have been harvested since at least 1955 (Figs. 8, 9). Except for influences of the exceptionally large 1951 and 1958 year classes, most of the catches sampled for age have been dominated by age 2 relative to biomass, and ages 1 and 2 relative to numbers. Major numerical but minor biomass contributions have been evident for age-0 fish. Inferences of the fishery's high dependency on younger age groups can be traced back to 1940. Given that the population distributes itself by age and size along the Atlantic coast, the quantity of landings and degree of effort expended in areas where younger and smaller fish predominate suggests a similar age composition for total catches during the presampling period (Figs. 3, 5).

Landings in the middle Atlantic area dominated the fishery in earlier years, but a shift had occurred by 1964, at which time Chesapeake Bay landings began to dominate (Fig. 4). Responding to a reduced population of larger and older fish, the industry increased the proportion of fishing effort exerted in areas closer to the large nursery areas of Chesapeake Bay and the south Atlantic area. Further, the fishery shifted from one that harvested the larger age 1's and 2's, and older fish, to one that harvests the smaller and younger fish. The larger, older fish were and still are vulnerable to the fishery during their fall migrations, but effort on these fish appears to be reduced within the north Atlantic and middle Atlantic areas.

A comparison of age-specific estimates of exploitation rates supports the earlier discussion on age dependency, population sizes, and age structure (Fig. 26). In the mid-1950's, the exploitation rates, although varying, were lower than those

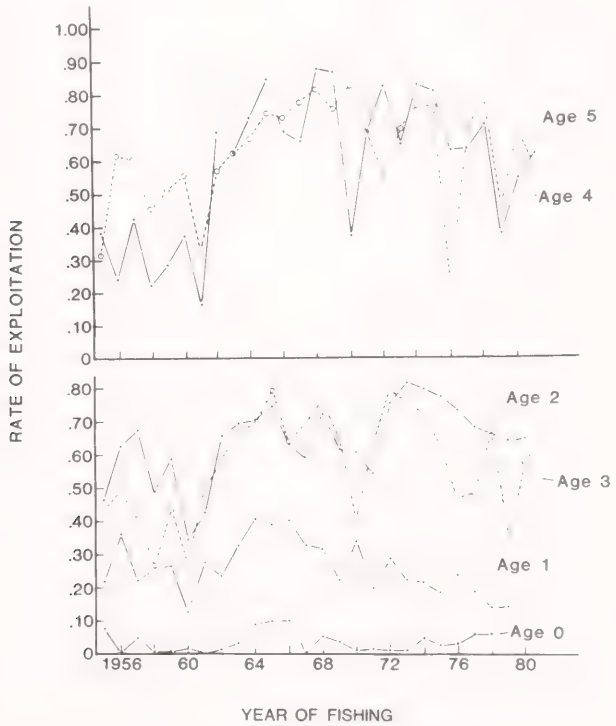

FIGURE 26.—Estimates of annual rates of exploitation of Atlantic menhaden, ages 0 through 5.

for the subsequent years when population size was decreasing. The rates reached their lowest points for ages 1-3 during 1960, when the 1958 year class was fully recruited. A low point followed for ages 4 and 5 during 1961. All exploitation rates generally increased during the low recruitment years of the 1960's, and began decreasing during the 1970's as the population size began to increase due to higher recruitment. The rate of reduction noted for nominal effort (Fig. 1) lagged behind that of the stock and was apparently too slow to prevent the observed rise in exploitation rates during the 1960's.

The exploitation rates of age-2 fish appear to have progressively declined during the later 1970's, following a disproportionately large increase after 1971. This increase apparently was a product of a shift in the pattern of fishing that occurred during the regrowth of the fishery and that pattern still exists. Although slightly lagging behind that of the age-2 fish, exploitation rates on age-0 fish began increasing by 1974, and reached an alarming rate of about 15% in 1979 (preliminary estimate). This rate of exploitation occurred in virtually one quarter of fishing and slightly exceeded the rate of exploitation for age-1 fish for the entire season. The disproportionately low exploitation rate on age 1's is probably due to their increasingly smaller size, a consequence of which would be a more southerly distribution. Additionally, many would remain in or near estuarine nursery areas and surrounding smaller bays and sounds, and thus be less available to the fishery.

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DENSITY AND DEPTH DISTRIBUTION OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, AND SPOT, *LEIOSTOMUS XANTHURUS*, IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Densities of larval gulf menhaden, *Brevoortia patronus;* Atlantic croaker, *Micropogonias undulatus;* and spot, *Leiostomus xanthurus,* compared among three transects in the northern Gulf of Mexico, indicated that all three species were more abundant at inshore (18 m isobath) than offshore stations (91 and 183 m isobaths). Gulf menhaden and Atlantic croaker were most abundant off Southwest Pass, Louisiana, a major outlet of the Mississippi River into the Gulf of Mexico. Gulf menhaden larvae caught at inshore stations were larger than those collected at offshore stations. Of the three species, only gulf menhaden showed any consistent pattern in vertical distribution. At inshore stations, gulf menhaden were concentrated near the surface at midday, but distributed across sampling depths (1 m, 6 m, and 12 m) at dawn, dusk, and midnight, a pattern opposite to that typically reported for larval fish. At offshore stations (with sampling depths of 1 m, 30 m, and 70 m), gulf menhaden larvae were present at 70 m, but most were caught near the surface. A concentration in surface waters was again most pronounced at midday.

Gulf menhaden, *Brevoortia patronus;* spot, *Leiostomus xanthurus;* and Atlantic croaker, *Micropogonias undulatus,* are thought to spawn offshore in winter months in the northern Gulf of Mexico (Nelson 1969; Fore 1970; Diaz 1982; Christmas et al. 1982). Larvae of the three species are transported inshore to nursery grounds in marshes and estuaries along the northern coast. One passive mechanism suggested for movement of gulf menhaden includes longshore advective transport, entrainment into the coastal boundary layer, and eventual transport into the estuary effected by the seasonal rise of sea level in spring (Shaw et al. 1985a). The passage of winter cold fronts can also be expected to influence transport.

Spawning of gulf menhaden occurs in shelf waters out to at least 91 m (Guillory et al. 1983), but is concentrated around the Mississippi River Delta (Fore 1970). Atlantic croaker apparently spawn in waters <54 m in depth (Diaz 1982), while spot spawn in waters >27 m (Dawson 1958; Nelson 1969). Gulf menhaden larvae spend 3 to 5 weeks at sea before entering estuaries when they are 12 to 25 mm in length (Reintjes 1970; Christmas and Etzold 1977; Guillory et al. 1983).

Fish larvae are nonrandom in their spatial distribution in both the vertical and horizontal dimensions. One primary influence on the vertical distribution of larvae is their diel vertical movement (migration) in the water column; larvae of many species rise to the surface by night and descend by day (e.g., Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). Horizontal distribution is also dynamic, with dispersion and aggregation of larvae affected by such factors as adult spawning behavior, water mass movements, localized larval mortality, and larval behavior (Smith 1981; Houde 1982; Jahn and Lavenberg 1986).

In this study we examined the density and depth distribution of larval gulf menhaden, spot, and Atlantic croaker at three locations in the northern Gulf of Mexico, with emphasis on the area around Southwest Pass, LA, the main discharge of the Mississippi River among the delta distributaries. Size distributions of gulf menhaden were compared to determine if inshore larvae were older than offshore larvae, the expected pattern if adults are spawning primarily offshore and larvae are moving inshore.

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METHODS

Larvae were collected along three inshore-offshore transects (off Southwest Pass, LA; Cape San Blas, FL; and Galveston, TX) at stations positioned over the 18 m (10 fm), 91 m (50 fm), and 183 m (100 fm) isobaths (Fig. 1). Sampling took place on four cruises in December 1979, February 1980, December 1980, and February 1981. Collections were made with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1976). The MOCNESS consisted of nine 505 μm mesh Nitex[3] plankton nets with mouth openings of 1 m by 1.4 m. Due to equipment problems, only the inshore Southwest Pass station was sampled on the first cruise. Galveston stations were added to the sampling program on the February 1981 cruise.

MOCNESS nets were deployed in the following manner: Net 1 remained open as the MOCNESS descended from the surface to the deepest depth to be sampled. Nets 2 and 3 sampled at that depth, one at a time, and net 4 opened as the MOCNESS was raised to an intermediate depth, where nets 5 and 6 sampled. Net 7 was open while the MOCNESS was brought to the surface, where nets 8 and 9 fished. Discrete depth nets generally fished from 2 to 3 minutes before deployment of the next net. Sampling depths were approximately 12, 6, and 1 m at inshore stations and 70, 30, and 1 m at the offshore stations. At each station, MOCNESS casts were made at 0600, 1200, 1800, and 2400 h, with a towing speed of approximately 2 nmi/hour. Sensors on the MOCNESS provided continuous recording of temperature and depth. Two flowmeters, one mounted on top of the MOCNESS and one within the net opening, were used to calculate the volume of water sampled by each net and to detect net clogging. The mean volume filtered by each discrete depth net was 140 m^3 (SD = 101.2, n = 529).

The collection of one net at each discrete depth was preserved in 5% buffered formalin-seawater and the collection of the other was preserved in 70% ethanol. Formalin-preserved larvae were used in gut content analysis (Govoni et al. 1983), and alcohol-preserved larvae were used in otolith analysis of age and growth (Warlen in prep[4]). In the laboratory all fish larvae were removed from

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[4]S. M. Warlen. Manuscr. in prep. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

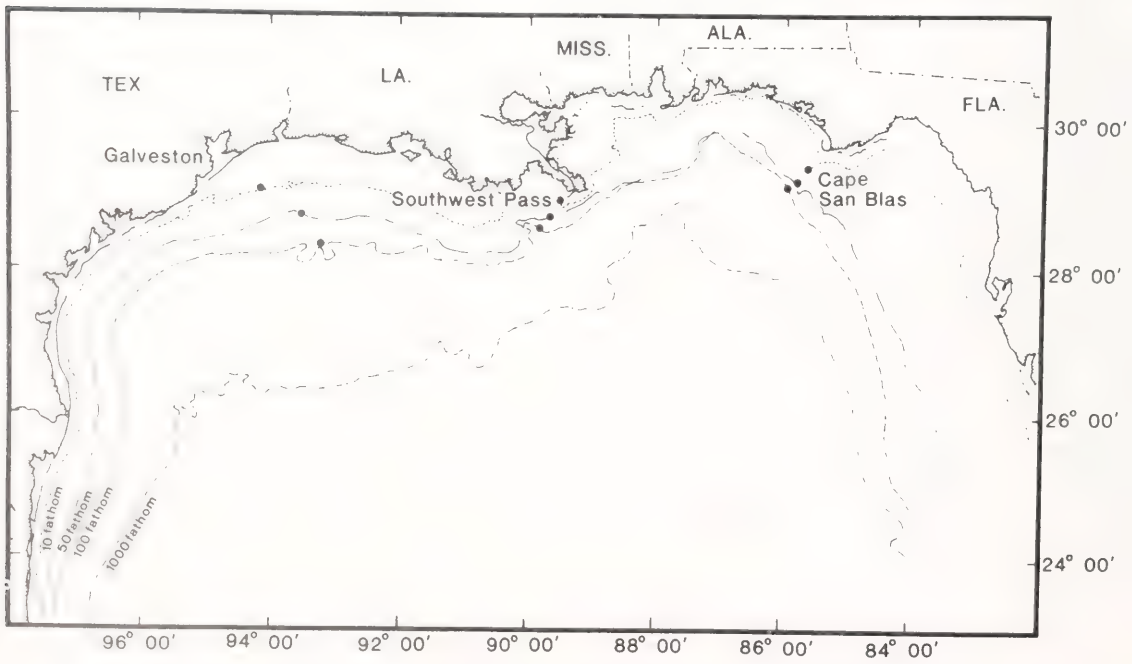

FIGURE 1.—Location of sampling transects and stations in the northern Gulf of Mexico.

the samples and counted. Gulf menhaden were measured (standard or notochord length) to the nearest 0.01 mm with an ocular micrometer. When more than 30 menhaden occurred in a sample, 30 individuals were randomly selected and measured (length measurements were not corrected for shrinkage). Due to the scarcity of larvae at outer stations, menhaden from both the 91 and 183 m Southwest Pass stations were combined in the comparison of offshore size distribution with inshore (restricted to the Southwest Pass station to allow valid comparison). Spot and Atlantic croaker were too rare at all offshore stations to allow size comparisons.

Analysis of vertical movement was based on the mean percentage of larvae caught at each of three discrete depths on each MOCNESS cast, allowing comparison among casts with widely varying densities of larvae. Gulf menhaden caught at the inshore stations were divided into three size classes to determine if vertical distribution varied with age. Because of the low number of larvae at the 183 m stations (see above), analysis of offshore vertical distribution was based on MOCNESS casts from both the 91 and 183 m stations. Mean densities at each depth were also calculated for each time of sampling.

RESULTS

Overall densities (number $\times$ 100 m^{-3}) of gulf menhaden, spot, Atlantic croaker, and the total of all species (these three species plus all others, including damaged and unidentifiable clupeids that may have been gulf menhaden) varied widely among cruises, stations, times, and depths. The majority of the 529 net tows did not catch any gulf menhaden (67%), spot (83%), or Atlantic croaker (82%). Smaller individuals of all three species, however, were probably not retained by the 505 μm mesh nets. In all but four cases, gulf menhaden were more abundant than spot or Atlantic croaker (Table 1). The density of all three species was generally greatest at the inshore (18 m) stations and declined offshore, with low or zero densities common at both offshore stations of Cape San Blas and Galveston (Table 1).

Gulf menhaden were most abundant at the Southwest Pass stations, except on the December 1980 cruise, when they were most abundant at the 18 m Cape San Blas station (Table 1). Atlantic croaker larvae were most abundant at the inshore Southwest Pass station in December 1980 and February 1981, but not in February 1980. Spot

TABLE 1.—Mean densities (SD in parentheses) of ichthyoplankton (larvae $\times$ 100 m^{-3}) collected at three stations at three sites in the northern Gulf of Mexico. Densities are averaged over three discrete depths and four times of day. Station 1 was over the 18 m isobath, station 2 over the 91 m isobath, and station 3 over the 183 m isobath. n = number of net tows. "Total larvae" includes the three target species and all others.

Cruise	Station	n	Total larvae	Gulf menhaden	Spot	Atlantic croaker
Dec. 1979	SW Pass 1	24	78.5 (88.9)	43.7 (66.9)	1.3 (2.3)	3.5 (3.9)
Feb. 1980	SW Pass 1	24	228.7 (281.4)	79.3 (122.5)	1.1 (0.3)	0.1 (0.3)
	SW Pass 2	23	32.1 (43.0)	7.4 (16.0)	0	0
	SW Pass 3	7	7.5 (5.9)	0.4 (0.7)	0	0
	San Blas 1	24	20.0 (14.4)	0.2 (10.5)	0.6 (0.9)	0.6 (0.8)
	San Blas 2	23	114.3 (85.3)	0.1 (0.2)	0.1 (0.3)	0.1 (0.4)
	San Blas 3	16	18.4 (13.2)	0	0	0
Dec. 1980	SW Pass 1	35	38.4 (30.4)	6.0 (8.0)	0.1 (0.2)	9.1 (15.2)
	SW Pass 2	24	56.0 (55.5)	8.8 (18.3)	0.2 (0.6)	3.1 (7.8)
	SW Pass 3	24	43.7 (38.4)	0.7 (2.1)	0	0
	San Blas 1	24	330.5 (618.6)	14.1 (42.4)	98.1 (259.3)	0.1 (0.1)
	San Blas 2	24	112.8 (83.2)	0	0.5 (1.2)	0.1 (0.3)
	San Blas 3	24	55.1 (61.0)	0	0	0
Feb. 1981	SW Pass 1	23	36.7 (49.7)	26.8 (43.8)	0.6 (0.9)	1.8 (2.6)
	SW Pass 2	22	65.8 (69.1)	13.6 (17.5)	0.6 (0.9)	0.6 (1.2)
	SW Pass 3	24	18.6 (15.0)	6.2 (11.8)	0.1 (0.1)	0
	San Blas 1	23	28.7 (15.8)	0	0	0
	San Blas 2	24	10.0 (9.0)	0	0	0
	San Blas 3	24	9.3 (6.8)	0	0	0
	Galveston 1	23	53.2 (26.1)	9.3 (6.8)	0	0
	Galveston 2	24	87.1 (65.0)	0.1 (0.1)	0	0
	Galveston 3	24	22.1 (16.4)	0	0	0

larvae were never very abundant except at the inshore San Blas station on the December 1980 cruise (Table 1), when a single dense patch of larvae was encountered on two successive MOCNESS casts (Govoni et al. 1985). Densities were as high as 993 larvae × 100 m^{-3}, an abundance not observed for other species and not approached by spot densities in any other sample. On the February 1981 cruise, no spot larvae were collected at this station. The occurrence of this aggregation, then, appeared to be a reflection of patchiness rather than geography.

An inshore-offshore comparison (Southwest Pass stations) of menhaden lengths revealed that on two of three cruises (February 1980 and December 1980) larvae were larger at the inshore station (Table 2). This was not the case on the third cruise, however, when mean lengths were similar. Results of a two-way ANOVA (Table 2) indicated significant differences in mean length for both main effects of station and cruise and for their interaction ($P < 0.001$). Thus, the pattern to the data is more complex than can be summarized by main effects alone. Length-frequency distributions indicated a bimodal pattern at the inshore station with most larvae in the larger size mode (Fig. 2). Larger larvae were not as common at the offshore stations except on the final cruise, when a bimodal pattern occurred offshore as well as inshore.

At the inshore stations, total larvae were generally distributed evenly among the three sampling depths at all times of day (Fig. 3), although

TABLE 2.—Mean standard length (mm, SE in parentheses) of gulf menhaden caught on three cruises at inshore (18 m isobath) and combined offshore (91 and 183 m isobaths) stations off Southwest Pass, LA. *F* values are results of a two-way ANOVA comparing lengths among cruises and between stations.

	Station		*F*		
Cruise	Inshore	Offshore	Cruise	Station	Cruise × Station
Feb. 1980	15.2 (0.3)	8.9 (0.2)	21.8**	81.8**	62.6**
Dec. 1980	13.5 (0.3)	8.7 (0.3)			
Feb. 1981	12.3 (0.2)	12.3 (0.2)			

**$P < 0.001$.

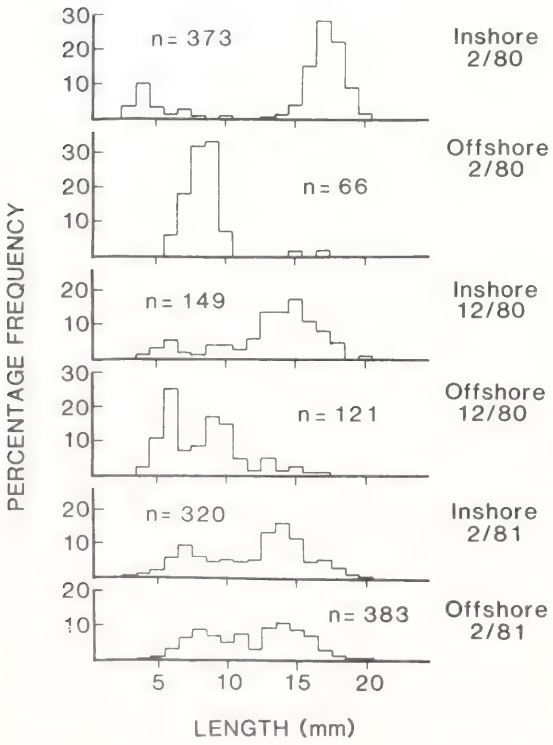

FIGURE 2.—Length-frequency distributions of gulf menhaden larvae collected from inshore (18 m isobath) and offshore (91 and 183 m isobaths combined) stations off Southwest Pass, Louisiana, on three cruises (February 1980, December 1980, and February 1981). n = number of larvae measured.

TABLE 3.—Mean density (larvae × 100 m^{-3}) at each discrete depth during each time period. MOCNESS casts in which no larvae of the target species were caught at any of the discrete depths were not included in calculation of means.

	Time			
Station/species	0600	1200	1800	2400
Inshore				
Total larvae				
1 m	68.23	120.97	341.10	76.36
6 m	56.01	25.76	144.20	86.82
12 m	42.44	25.24	69.20	173.78
Gulf menhaden				
1 m	31.72	37.35	48.83	12.44
6 m	4.54	0.14	101.06	22.74
12 m	13.16	0.60	29.93	22.37
Spot				
1 m	1.36	1.99	154.35	8.13
6 m	0.76	1.04	2.02	5.12
12 m	0.82	0.39	1.79	34.63
Atlantic croaker				
1 m	2.05	1.07	2.47	1.62
6 m	4.08	4.05	3.61	1.66
12 m	12.65	1.32	4.57	6.43
Offshore				
Total larvae				
1 m	103.90	57.37	57.64	49.65
30 m	35.41	21.30	63.37	42.37
70 m	23.38	8.35	14.93	14.29
Gulf menhaden				
1 m	23.70	35.60	14.36	14.19
30 m	7.47	0.00	7.77	3.76
70 m	0.22	0.39	0.42	0.29

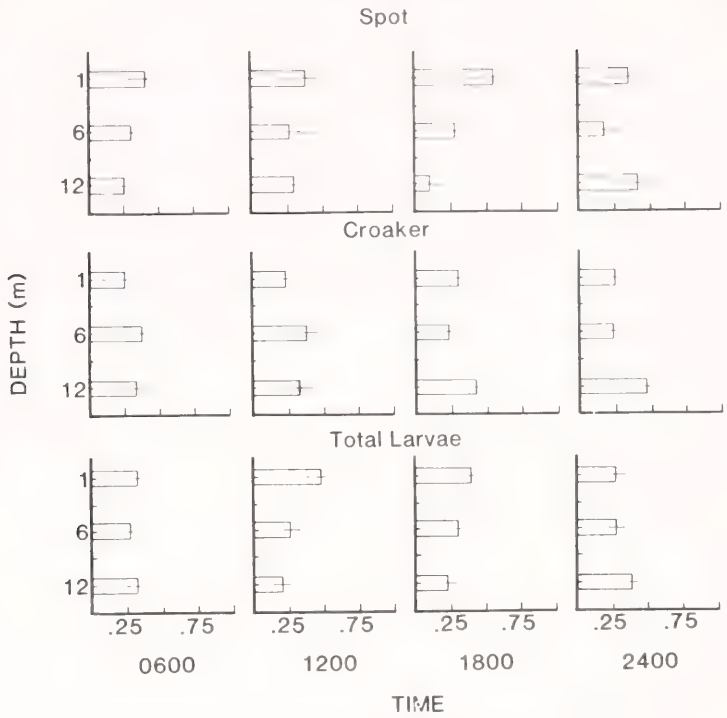

FIGURE 3.—Mean percentage of Atlantic croaker, spot, and total larvae collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

mean densities were greater in surface waters at 1200 and 1800 h and in deeper waters at 2400 h (Table 3). The high mean densities of spot in surface waters at 1800 h and at 12 m at 2400 h (Table 3) were related to the encounter with the previously mentioned patch of larvae at Cape San Blas. When mean relative proportions were considered, however, these trends were moderated (Fig. 3). Although mean densities suggested a propensity for Atlantic croaker larvae to occur in deeper waters (Table 3), this trend also weakened when relative proportions were considered (Fig. 3). Gulf menhaden larvae in all three length groups were highly concentrated at the surface at 1200 h, but showed inconsistent patterns at other times (Fig. 4).

At the offshore stations (91 and 183 m), where there was a broader scale for vertical distribution, total larvae were generally less abundant at the deepest sampling depth (70 m, Table 3), but mean relative distributions indicated only slight trends (Fig. 5). Gulf menhaden larvae at offshore stations had greater densities at the surface at all times, with few larvae present at 70 m (Table 3). They again occurred almost exclusively in surface samples at 1200 h (Fig. 5). (Spot and Atlantic croaker were too rare at the offshore stations to allow examination of vertical distribution.)

Comparison of MOCNESS casts in thermally stratified versus isothermal water columns indicated that the presence of a weak thermocline did not inhibit vertical movement by any of the three target species or total fish larvae. Depth distributions were similar regardless of the thermal structure of the water. In most cases where a thermocline occurred, it was reversed, with colder water overlying warmer water, and a temperature difference of $<5^{\circ}$C, the result of the Mississippi River plume.

DISCUSSION

High densities of gulf menhaden larvae at the Southwest Pass stations support the conclusions of Fore (1970) and Christmas and Waller (1975[5]) that spawning is concentrated around the Missis-

[5]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr. Gulf Coast Laboratory, Ocean Springs, MS 39564.

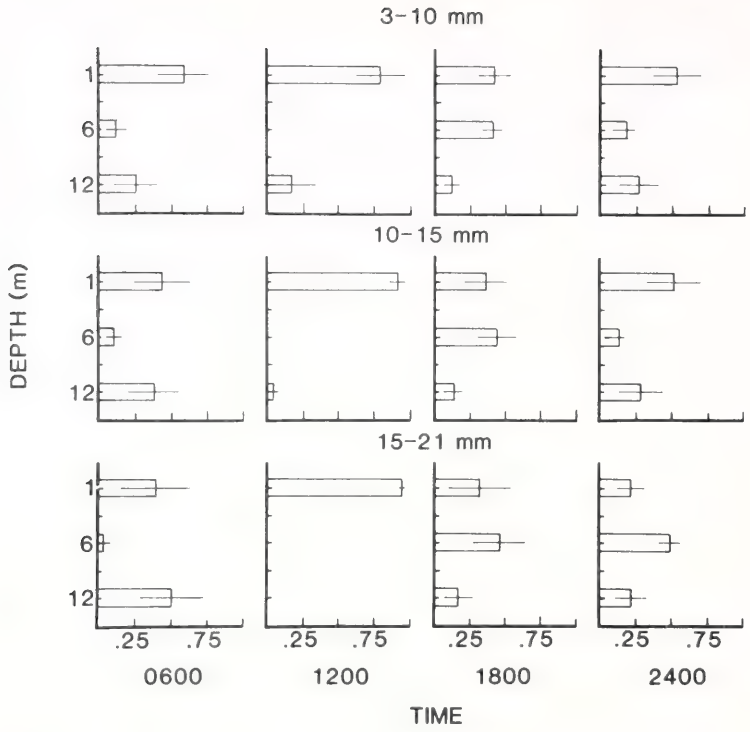

FIGURE 4.—Mean percentage of gulf menhaden larvae, divided into three size groups, collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

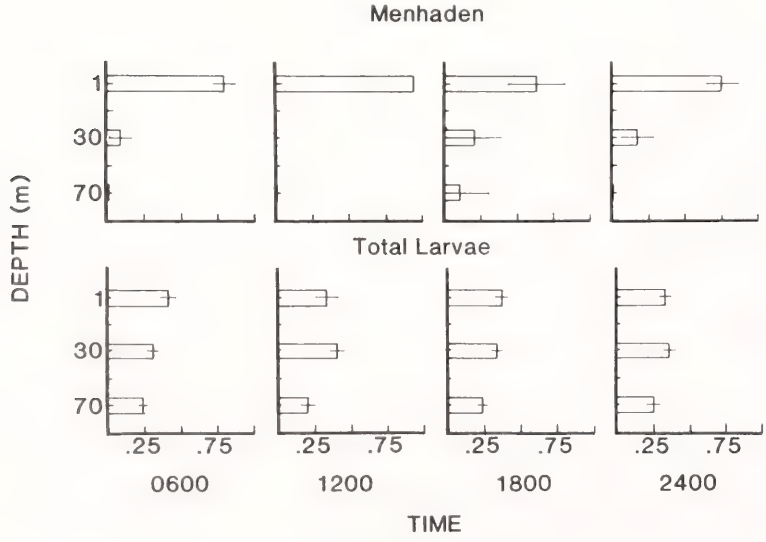

FIGURE 5.—Mean percentage of gulf menhaden and total larvae collected at three discrete depths at offshore stations (91 and 183 m isobaths). Error bars are standard errors.

sippi River Delta. In addition, Atlantic croaker larvae were rarely caught except at the inshore Southwest Pass station. High levels of nutrients (Riley 1937) and the resultant high plankton biomass in this region (Bogdanov et al. 1968) may make conditions exceptionally favorable for fish larvae.

Densities of all three target species showed a clear decline from inshore to offshore waters (Table 1). Shaw et al. (1985b) found a similar pattern for gulf menhaden larvae farther west along the Louisiana coast; densities were greatest in waters between the 14 and 24 m isobaths, with a shift in concentration to very nearshore waters by the end of the spawning season. The major spawning efforts of gulf menhaden, spot, and Atlantic croaker appear to occur in a relatively narrow band along the coast.

Size-frequency distributions of gulf menhaden larvae along the Southwest Pass transect showed that offshore stations were populated with smaller larvae on two of three cruises (Fig. 2, Table 2), but off western Louisiana, Shaw et al. (1985a) detected no difference in the size distribution of gulf menhaden from the 183 m isobath to inshore waters, except at stations immediately adjacent to shore (approximately 9 m in depth). Our observed pattern of decreasing size with distance from shore could arise either by adults spawning offshore and larvae growing as they move toward estuarine nursery grounds, or from serial spawning as adults move offshore during the protracted spawning season. The latter pattern is corroborated by Roithmayr and Waller (1963) and Fore (1970).

Only gulf menhaden showed clear evidence of a diel pattern in vertical distribution; they were concentrated almost exclusively at the surface at midday, but were more vertically dispersed at night at inshore stations. Size did not determine which larvae descended by dusk, because the vertical distribution was similar across all three size groups. In contrast, vertical migration of yellowtail flounder, *Limanda ferruginea,* and Atlantic herring, *Clupea harengus,* larvae varies with size, with smaller individuals remaining closer to the water surface (Smith et al. 1978; Wood 1971). Depth distributions of northern anchovy, *Engraulis mordax,* and white croaker, *Genyonemus lineatus,* also vary with age, with older larvae concentrating in deeper waters (Brewer and Kleppel 1986).

Gulf menhaden larvae >12 mm SL have deflated swimbladders by day and inflated swimbladders at night, achieved by swallowing air at the surface (Hoss and Phonlor 1984). This behavior, common among clupeoids (Hunter and Sanchez 1976; Uotani 1973), is thought to allow passive depth maintenance during nonfeeding hours at night (Hunter and Sanchez 1976). The observed depth distribution of gulf menhaden indicates that larvae must actively swim to stay at the surface during daylight hours. Apparently, the larvae slowly sink at night despite having gas in their swimbladders, and are, therefore, distributed at various depths. Data from offshore stations (Fig. 4) suggests, however, that most larvae are able to maintain their position within the upper 30 m of the water column.

The pattern of vertical distribution of gulf menhaden is opposite of that reported for numerous other species, in which larvae rise toward the surface at night and descend by day (e.g., Seliverstov 1974; Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). A reversed pattern has also been observed for *Gadus macrocephalus* (Boehlert et al. 1985) and *Ammodytes personatus* (Yamashita et al. 1985). Yamashita et al. (1985) suggested that diurnal feeding requirements and nocturnal avoidance of upwardly migrating predators influence the vertical migration of *Ammodytes.* The behavior of Atlantic menhaden, *Brevoortia tyrannus,* is probably similar to gulf menhaden, as they are also reported to be more concentrated in surface waters by day than night (Thayer et al. 1983).

The presence of a weak thermocline with a gradient of <5°C did not appear to influence the vertical movement of fish larvae in this study. Other studies have reached conflicting conclusions. Ahlstrom (1959) and Loeb (1980) found thermal stratification with a temperature difference of 8° to 10°C very important in determining vertical distribution. Smith et al. (1978), Kendall and Naplin (1981), and Sameoto (1982), however, found that thermal gradients of 8° to 14°C did not inhibit vertical migration. The depth of the water column, the intensity of temperature change at the thermocline, and behavior of the species in question likely influence migration patterns. In relatively shallow water (Smith et al. 1978; Kendall and Naplin 1981; this study), thermal stratification appears less of a barrier than in deeper water. In this study larvae of gulf menhaden, spot, and Atlantic croaker largely remained within the upper 30 m, even when the water column was well-mixed to a depth of over 100 m. As we found for gulf menhaden, Brewer

and Kleppel (1986) noted significant diurnal depth stratification of larvae in the absence of thermal stratification. Absolute depths may be more important than thermal layers in determining vertical distribution when temperature differences are small.

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DISTRIBUTION OF WITCH FLOUNDER, *GLYPTOCEPHALUS CYNOGLOSSUS*, IN THE SOUTHERN LABRADOR AND EASTERN NEWFOUNDLAND AREA AND CHANGES IN CERTAIN BIOLOGICAL PARAMETERS AFTER 20 YEARS OF EXPLOITATION

W R Bowering[1]

ABSTRACT

Witch flounder were distributed throughout the study area from Hamilton Inlet Bank to the Northern Grand Bank. The main concentrations were located in Hawke Channel, the channel around Funk Island Bank, and the north slopes of the Grand Bank. While these are believed to be the main locations of three separate stocks, there was no apparent discontinuity in the distribution among the three NAFO Divisions investigated. It is clear, however, that the stock located in NAFO Div. 3K is considerably larger than the combined stocks of NAFO Div. 2J and 3L. Stocks showed minimal variations in depth and temperature preference. Depth and temperature preferences were demonstrated for different size and age-classes of fish. There were substantial reductions in the number of age groups composing the stocks; this was complemented by increases in mean sizes at age for each stock although the magnitude of this increase varied from one stock to another. There was evidence of reduced size and age at sexual maturity in some instances, however, in most cases the results are difficult to explain. These changes in population dynamics are discussed in relation to changes in exploitation over the past 20 years.

Prior to the early 1960's, fishing for witch flounder, *Glyptocephalus cynoglossus*, in the area of southern Labrador and eastern Newfoundland was practically nonexistent. When a significant fishery began in the early 1960's, catches were taken from the accumulated virgin stock in NAFO (Northwest Atlantic Fisheries Organization) Div. 2J, 3K, and 3L (Fig. 1) primarily by large offshore otter trawlers from Canada, Poland, and the Soviet Union. Significant catches were also taken by Newfoundland gill net fishermen in the deepwater bays of northeastern Newfoundland (Bowering and Pitt 1974) (Fig. 1).

Annual landings increased dramatically from <1,000 t in 1963 to peak at nearly 24,000 t in 1973 (Fig. 2). It should be noted, however, that catch statistics prior to 1973 were based upon a formula for breaking down catches of unspecified flounder catches into species and may not be totally accurate. Subsequent to 1973, landings declined nearly as dramatically as they had risen until they stabilized at about 3,000-5,000 t annually over the period 1980-85. In 1973, ICNAF (International Commission for the Northwest Atlantic Fisheries) decided to place catch quota regulations on witch flounder in this area; for management purposes witch flounder in Div. 2J, 3K, and 3L was treated as a single unit (Fig. 1). The first TAC (total allowable catch) was placed on this stock in 1974 at a level of 22,000 t, which was subsequently reduced to 17,000 t for 1975-80, based upon an assessment by Bowering and Pitt (1974). An updated assessment by Bowering and Baird (1980) advised a TAC of 8,000 t for 1981, and this TAC level was in effect up to 1986. The TAC for 1987 was further reduced to 4,000 t.

Although, for management purposes, witch flounder in Div. 2J, 3K, and 3L is considered a single population (stock), stock delineation studies have shown this not to be the case. Fairbairn (1981), using biochemical systematics (electrophoresis), distinguished two separate breeding stocks in this area, one in Div. 3K and one in Div. 3L. No data were available from Div. 2J. Bowering and Misra (1982), employing a new multivariate analysis technique on meristic data, corroborated Fairbairn's (1981) findings and also identified a separate stock in Div. 2J.

The purpose of this paper is to describe the distribution of witch flounder throughout this management zone during recent years and to examine age, growth, and sexual maturity patterns by di-

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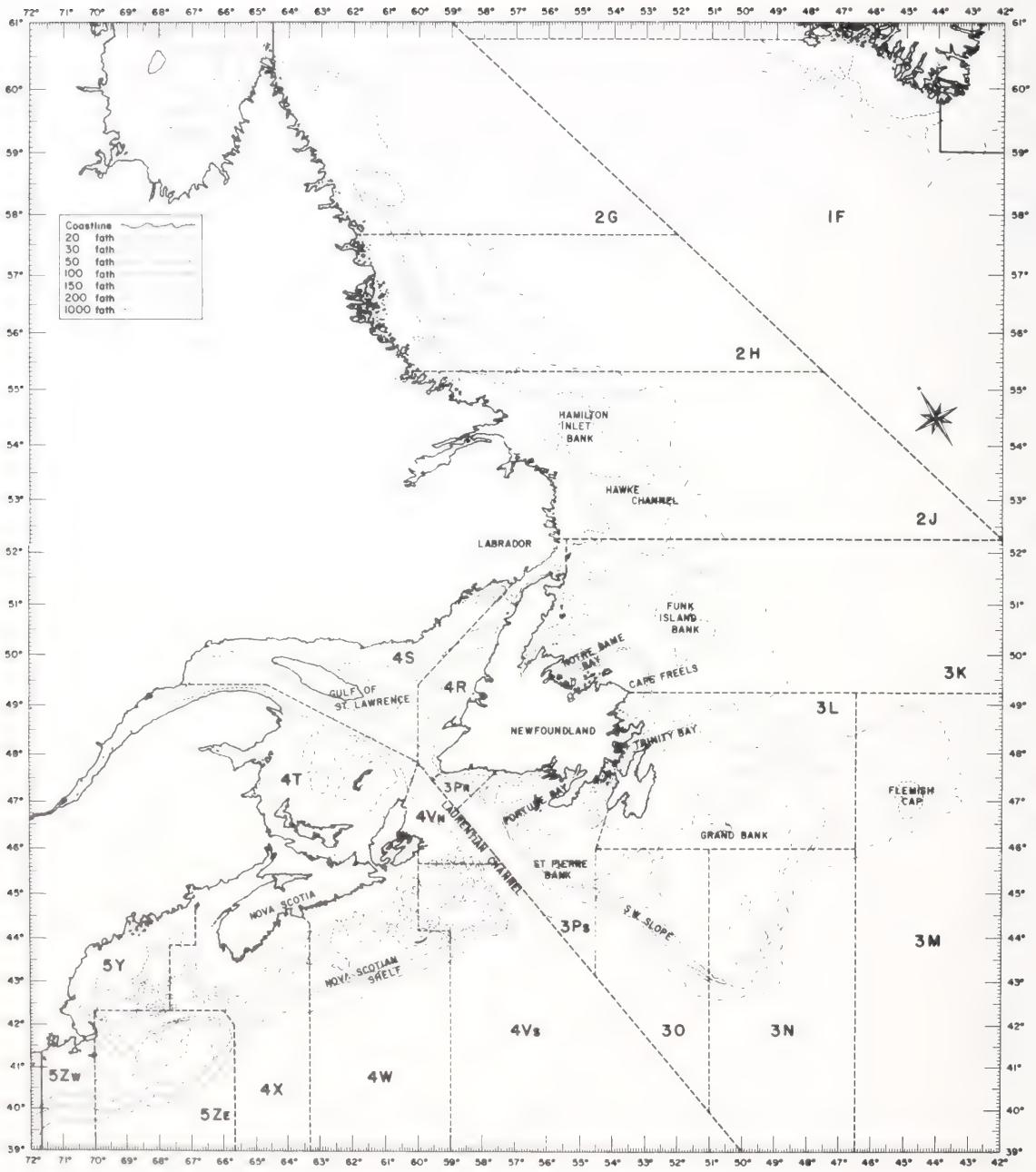

FIGURE 1.—Map of major place names mentioned in the text.

vision (since they contain different stocks) during, and subsequent to, years of heaviest exploitation.

MATERIALS AND METHODS

All data were collected during research vessel surveys for groundfish, carried out on an annual basis by Newfoundland-based research vessels or chartered vessels used for research purposes. All vessels used otter trawls with small mesh (12.7-28.1 mm) nylon liners in the cod end to prevent the escape of juvenile fish. Catch records of sets which experienced enough damage to the gear

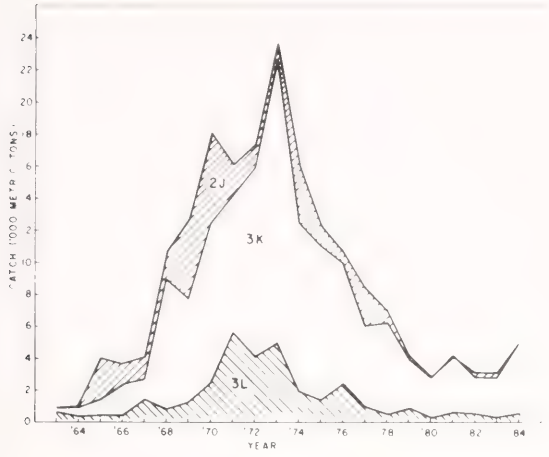

FIGURE 2.—Nominal catches of witch flounder in NAFO Div. 2J, 3K, and 3L from 1963 to 1984.

that overall catch might be affected were not included in the analyses. All fishing tows were of 30-min duration. At the end of each set, bottom temperature was measured using an expendable bathythermograph (XBT).

The geographic distribution and relative abundance is shown by indicating, in 1/2° latitude and 1° longitude rectangles, the average numbers of fish caught per 30-min set. A preliminary examination of distribution of witch flounder by year (all divisions) and season (Div. 3L only where enough seasonal data were available) showed no differences in geographic distribution; therefore, all trips were combined for the period 1977-83. These years were chosen for the distribution study since surveys during this period were based upon random distribution of sets throughout the fishing area whereas prior to this time some areas were surveyed using fixed station line transects not covering the whole area. The number of sets used in the presentation of the distribution is shown in Figure 3.

Ages were determined from otoliths (Powles and Kennedy 1967). Age composition is presented for males and females separately by division. Comparisons of age composition were made for Div. 2J for the periods 1973-78 and 1979-83, Div. 3K for the periods 1970-78 and 1979-83, and Div. 3L for the periods 1968-78 and 1979-83. For Div. 2J and 3K most data were collected during the last quarter, whereas for Div. 3L most data were collected over the last half of the year. However, considering the extent of the data and the very slow growth rate of witch flounder (Bowering 1976), slight differences in the timing of data collection are not sufficient to invalidate comparisons among divisions.

Growth (cm) was expressed in terms of log-log regressions ($\log_e$ Length $= a + b$ $\log_e$ Age (years)). Growth curves were computed for each of the age compositions stated above using data for each fish and not mean length at age. Differences in weight at age were then calculated between the earlier period and later period for each division by applying the length-weight relationship of Bowering and Stansbury (1984) to the observed mean length at age.

The maturity rates were calculated as the length (cm) and age (years) at which 50% of fish were mature (M_{50}) as determined by probit analysis according to the method of Bliss (1952) as applied to witch flounder in the Gulf of St. Lawrence by Bowering and Brodie (1984). The results are presented with 95% fiducial limits. Males for Div. 2J were not included in the calculations due to too low numbers of immature fish in the samples to allow for a significant probit analysis.

RESULTS

Geographic Distribution and Relative Abundance

Witch flounder was caught throughout the stock management zone of Div. 2J, 3K, and 3L from the northern tip of Hamilton Bank to the northern half of the Newfoundland Grand Bank (Fig. 4). Catches were insignificant in the Hamilton Bank area of Div. 2J with mean numbers per 30-min set generally <1.0. The general area of highest abundance in this division was to the south in the Hawke Channel. Here mean numbers per set ranged from about 2.0 in rectangle Q16 to 11.0 in P17, the highest in Div. 2J (Fig. 4). In Div. 3K, mean numbers per set per rectangle were considerably higher than those in Div. 2J. For many rectangles the mean numbers per set were in excess of 10.0. The general areas of highest abundance occurred along the deep waters around Funk Island Bank where mean catches ranged from about 13 to 53 fish/set. The highest density occurred in rectangles P21, P22, Q22, Q23, and R24 where mean catches ranged from 43 to 53 fish/set. In Div. 3L the only significant catches occurred along the northern slope and northeast cape of the Newfoundland Grand Bank. In this area, catches ranged from about 2 to

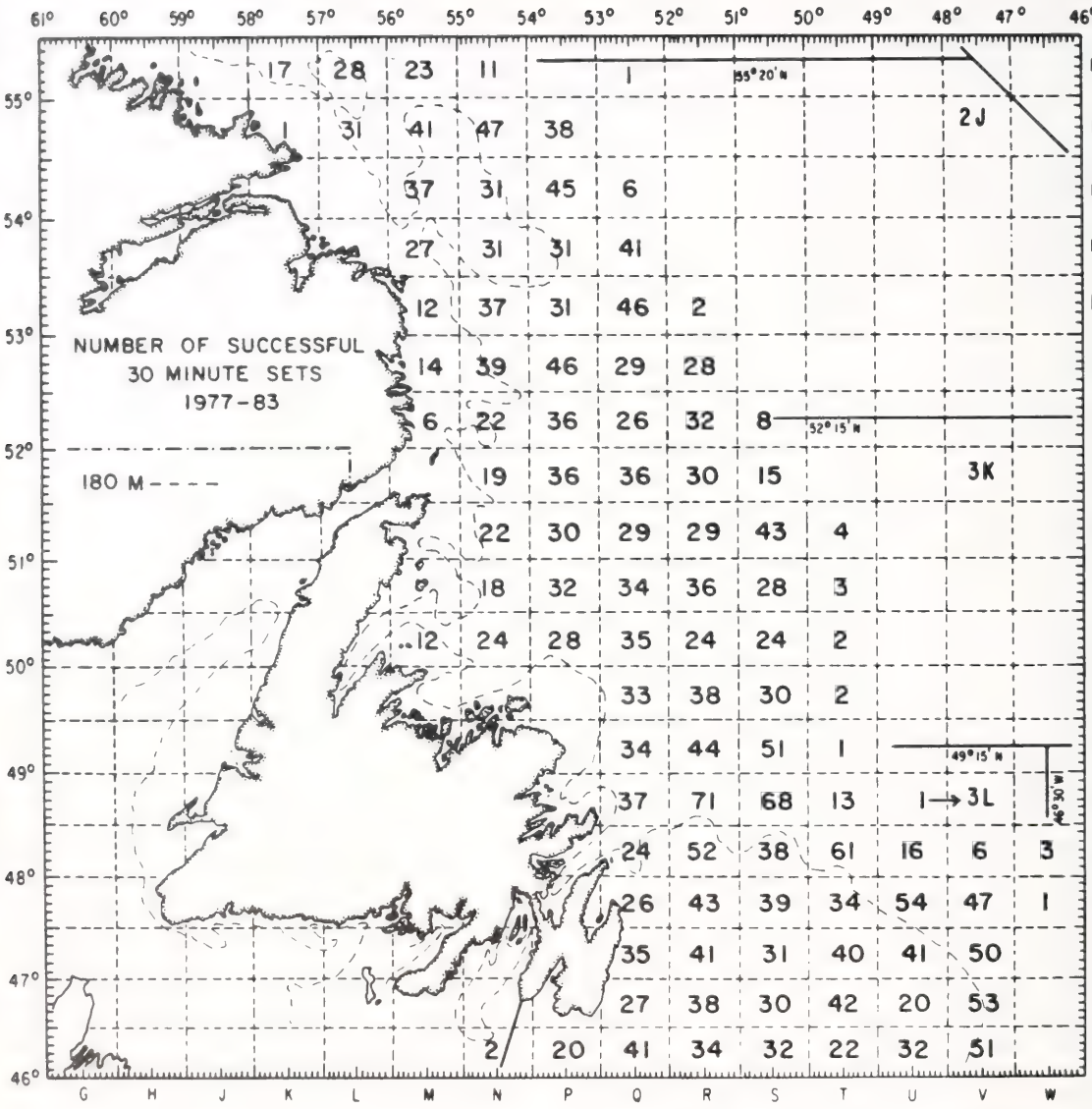

FIGURE 3. – Number of successful 30-min bottom trawl sets per (rectangle) in NAFO Div. 2J, 3K, and 3L by Canadian research vessels from 1977 to 1983.

15 fish. The highest mean catch was 23 and occurred in rectangle W27. This was based upon only 1 set however (Fig. 3). On the other hand, the second highest mean catch per set was 15 fish in the adjacent rectangle V27, based upon 47 sets (Figs. 3, 4). It should be noted also that some of the highest mean numbers per set occurred due east of Cape Freels along the dividing line between Div. 3K and 3L. Catches in the southern portion of Div. 3L were insignificant with most rectangles having mean catches of about 0.1 fish/set.

Distribution by Depth and Temperature

Distribution by 100 m depth intervals of witch flounder is presented in Figure 5. For Div. 2J, witch flounder were caught in depths ranging from 101 to 900 m. However, only the depth range

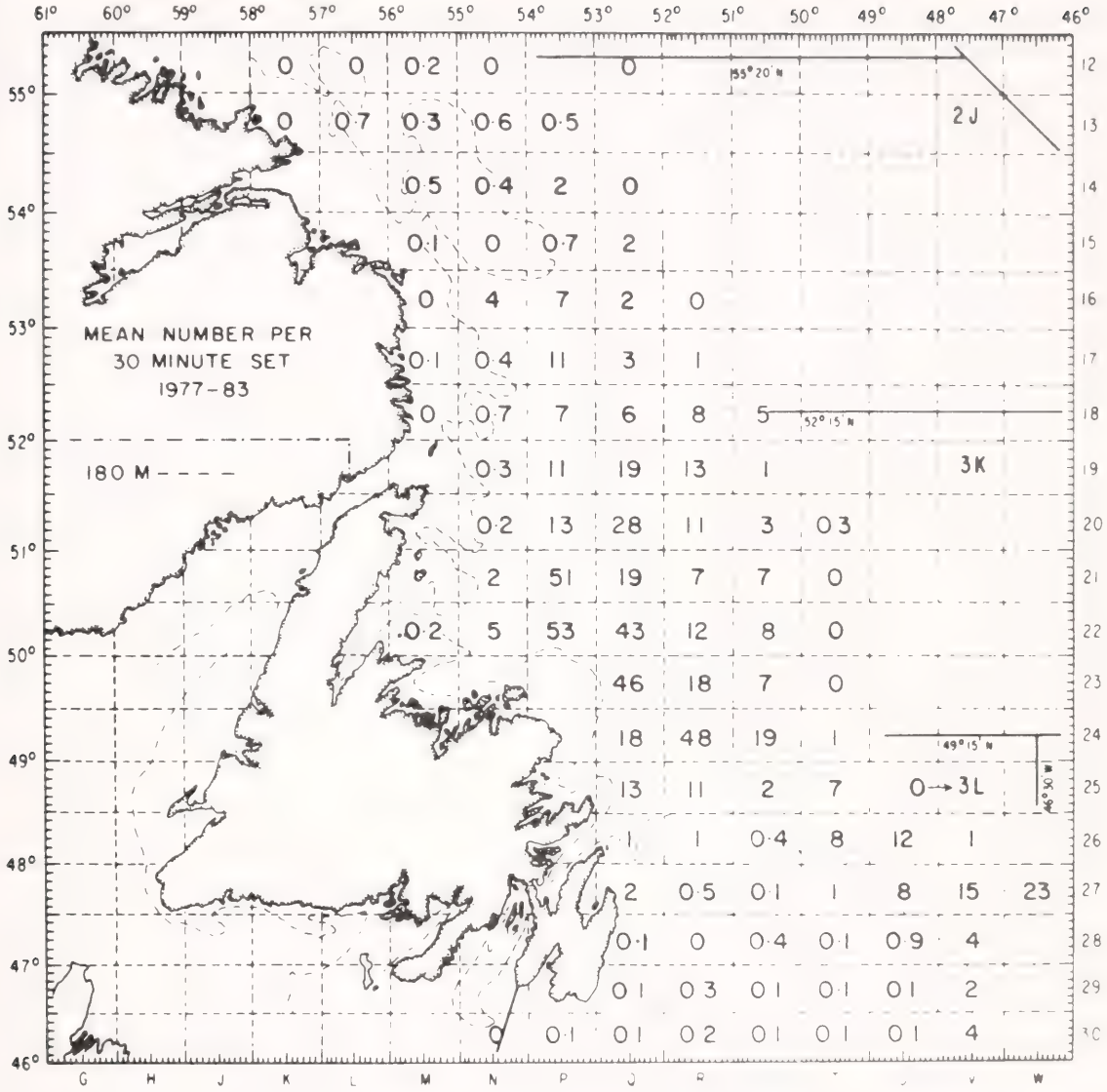

FIGURE 4.—Mean number of witch flounder caught per 30-min set per (rectangle) in NAFO Div. 2J, 3K, and 3L during 1977-83 by Canadian research vessels.

of 301-600 m showed any significant numbers with a peak at 501-600 m after which numbers declined rapidly to near zero. In Div. 3K witch flounder were caught in depths ranging from 201 to 900 m. Only one set was conducted in depths <201 m which yielded no catch (Fig. 5). The mean catch per set increased very sharply from this depth to peak at 401-500 m. The mean catch per set of about 47 fish at that depth interval was significantly different than mean catches in all other depths (Fig. 5). Mean catches beyond 500 m dropped off dramatically to near zero beyond 600 m. In Div. 3L witch flounder were caught in depths ranging from <101 to 800 m. No sets were conducted beyond 800 m (Fig. 5). Mean catches in depths <201 m were close to zero, based upon 864 sets. The increase in mean catch per set was similar to that of Div. 3K and peaked at 301-500 m, however, there was considerable overlap in confidence limits (Fig. 5). Unlike Div. 2J and 3K there

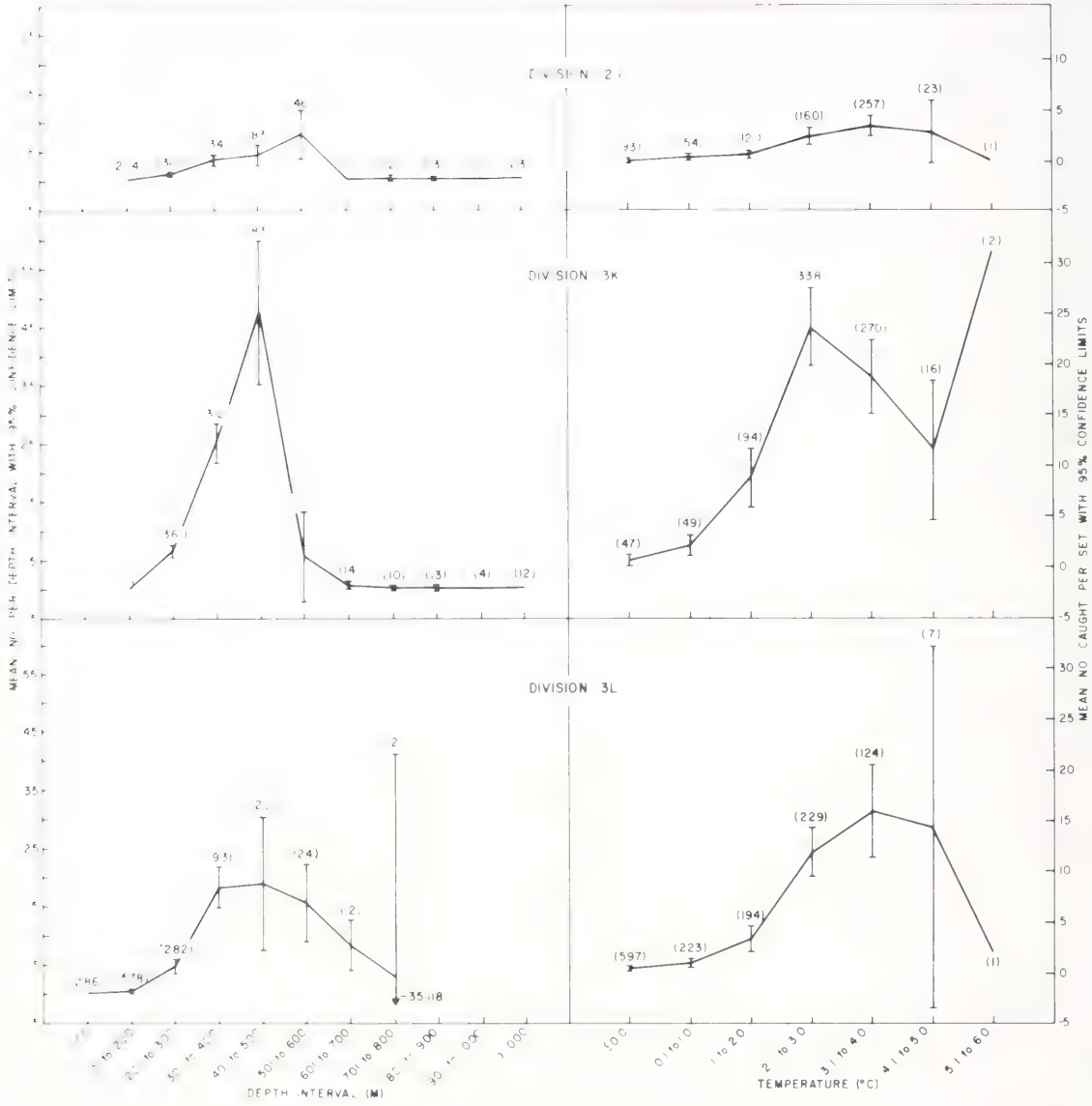

FIGURE 5.—Mean numbers of witch flounder caught per 30-min set per depth and temperature interval in NAFO Div. 2J, 3K, and 3L from 1977 to 1983 with 95% confidence limits. (Numbers in parentheses are number of sets observed.)

was not a marked decline in mean catch beyond the peak with substantial numbers of witch flounder being caught in depths up to 700 m.

Distribution of witch flounder by bottom temperature is also presented in Figure 5. Because of the very low catches in Div. 2J, it is difficult to identify discrete optimum temperatures. There was a slight increasing trend, however, from 1.1°-2.0°C to peak at 3.1°-4.0°C and decline beyond that. In Div. 3K witch flounder were caught in bottom temperatures from ≤0.0° to 6.0°C. There was a marked increasing trend from the 0.1°-1.0°C interval to peak at a temperature range of 2.1°-3.0°C beyond which the mean catch per set declined. The highest mean catch per set occurred at 5.1°-6.0°C. However, this resulted from one large catch in one of the two sets at this interval giving extremely wide 95% confidence limits. In Div. 3L an increasing trend was evidenced similar to that shown for Div. 3K, however, it was

slightly less marked and peaked at 3.1°-4.0°C and then declined. The data were too few at the higher temperatures to evaluate the significance of the decline.

Since depth and bottom temperature are generally related, a mean catch per 30-min set by depth and temperature is presented in Figure 6. When depth and bottom temperature are combined the range of best catches for Div. 2J is about 201-600 m and 2.1°-5.0°C. For Div. 3K it is about 201-500 m and 2.1°-4.0°C. For Div. 3L the range of best catches appears to be about 301-600 m and 2.1°-4.0°C. Despite the variations in depth and temperature distribution throughout the three divisions shown in Figures 5 and 6, the depth and temperature relationships among the divisions did not differ greatly or at least not among the locations fished (Fig. 7).

Mean length (cm) and mean age (years) for each depth and temperature interval are presented in Figures 8 and 9 respectively. Mean lengths and ages by depth interval for the three divisions showed similar trends in that they were highest in the shallower depths and declined to reach a low at some intermediate depth then increased and stabilized. For the three divisions combined there was a significant decrease in mean length from about 52 cm at ≤100 m to about 43 cm at 401-500 m. Mean lengths increased beyond this to near 47 cm and stabilized in the 600-900 m range. The mean age decreased from near 11 years old at ≤100 m to about 8 years old at 401-500 m. It stabilized at about 10 years old beyond that.

For all three divisions there was a general declining trend in mean length and age from the lower to intermediate temperatures (Fig. 9). In all cases (except Div. 2J where catches were generally low), the lowest mean size and age occurred at the 3.1°-4.0°C range. For the three divisions combined, there was a significant decline in mean length from about 50.5 cm and 10.0 years old in the 0.1°-1.0°C temperature range to about 45.5 cm and 9 years old in the 3.1°-4.0° temperature range. Beyond this range the mean length and age increased again.

Age Composition

The age compositions of male and female witch flounder by division and time period are presented in Figure 10. For Div. 2J during 1973-78,

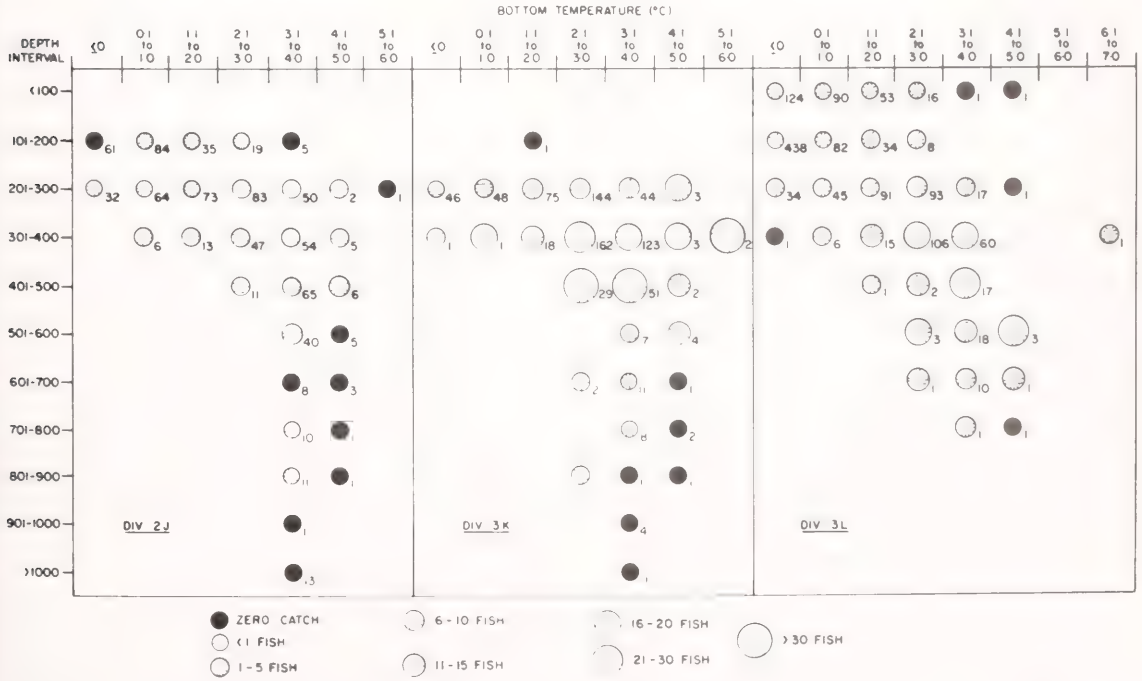

FIGURE 6.—Mean number of witch flounder caught per 30-min set by depth and temperature intervals in NAFO Div. 2J, 3K, and 3L from 1977 to 1983. (Numbers in parentheses are number of sets observed.)

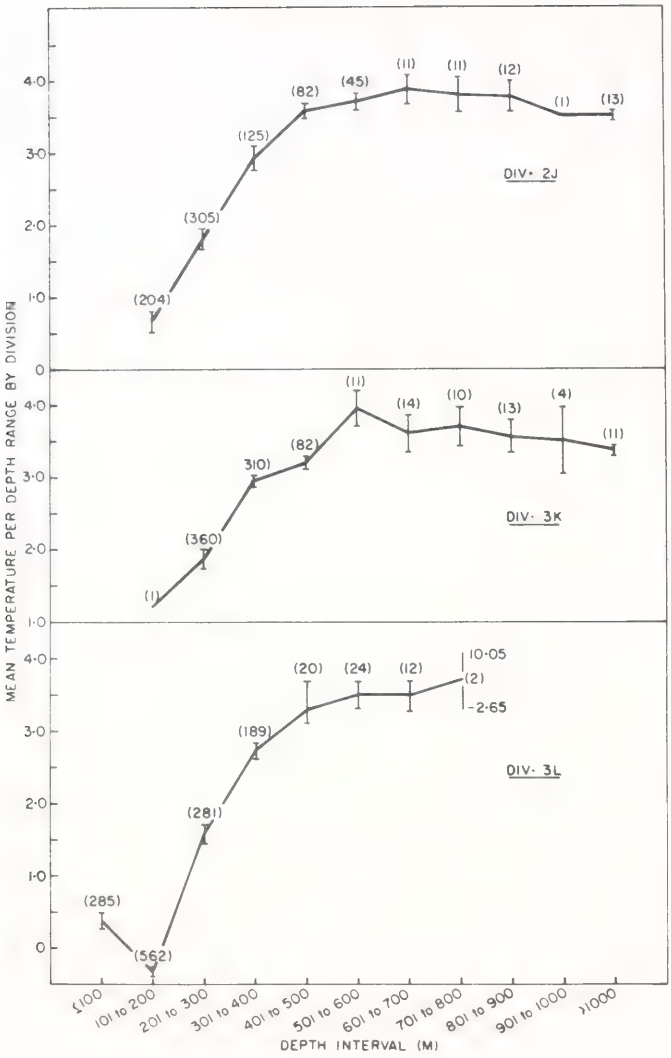

FIGURE 7.—Mean temperature with 95% confidence limits per depth interval in NAFO Div. 2J, 3K, and 3L from 1977 to 1983 as determined from research vessel surveys. The number of sets used in the calculations are shown in brackets for each depth interval.

males and females in the catches ranged from 6 to 18 years old and 4 to 21 years respectively. More than 50% of the males were older than age 10 and more than 50% of the females were older than age 12. In Div. 2J during 1979-83 the males and females ranged from 4 to 11 years old and 6 to 13 years old respectively. Less than 2% of the males were older than age 10 and less than 2% of the females were older than age 12.

For Div. 3K during 1970-78, males and females in the catches ranged from 3 to 16 years old and 3 to 22 years old respectively. About 50% of the males were older than 8 years while more than 50% of the females were older than 10 years. In Div. 3K during 1979-83 the males and females ranged from 2 to 13 years old and 2 to 14 years old respectively. About 30% of the males were older than 8 years with about 30% of the females older than 10 years.

In Div. 3L during 1968-78, males and females in the catches ranged from 2 to 18 years old and 4 to 23 years old respectively. About 50% of the males were older than 11 years and about 50% of the females were older than 12 years. During

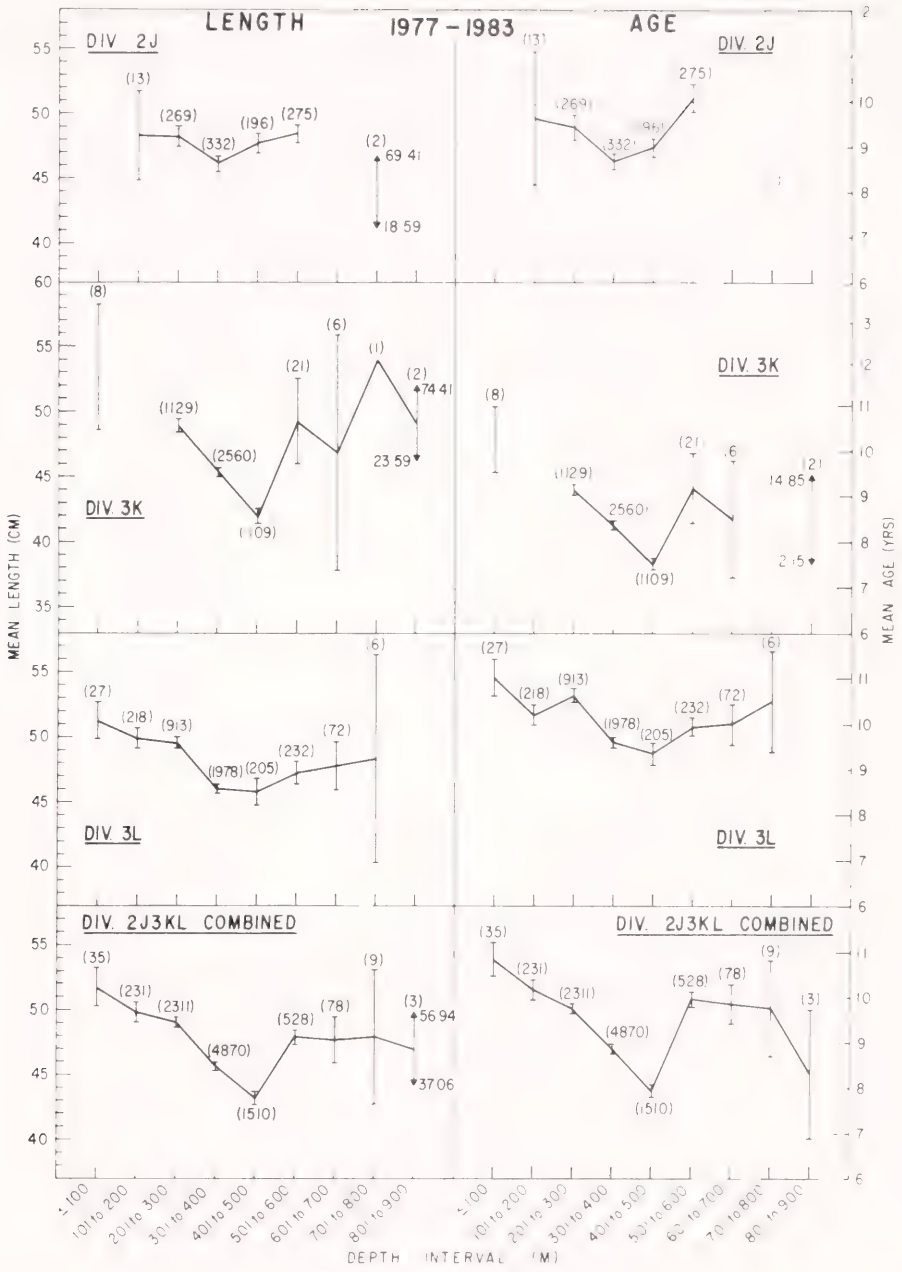

FIGURE 8.—Mean length (cm) and mean age (years) of witch flounder per depth interval in Div. 2J, 3K, and 3L separately and combined from research vessel surveys during 1977-83. (Number in brackets refers to the number of fish observed.)

1979-83 in Div. 3L, males and females ranged from 3 to 13 years old and 3 to 17 years old respectively. Only about 5% of the males were older than 11 years and about 8% of the females were older than 12 years.

Growth Curves

Growth curves of male and female witch flounder with mean lengths at age are presented in Figure 11 and Table 1. Clearly, males do not grow as fast as females over the life span. Growth rates

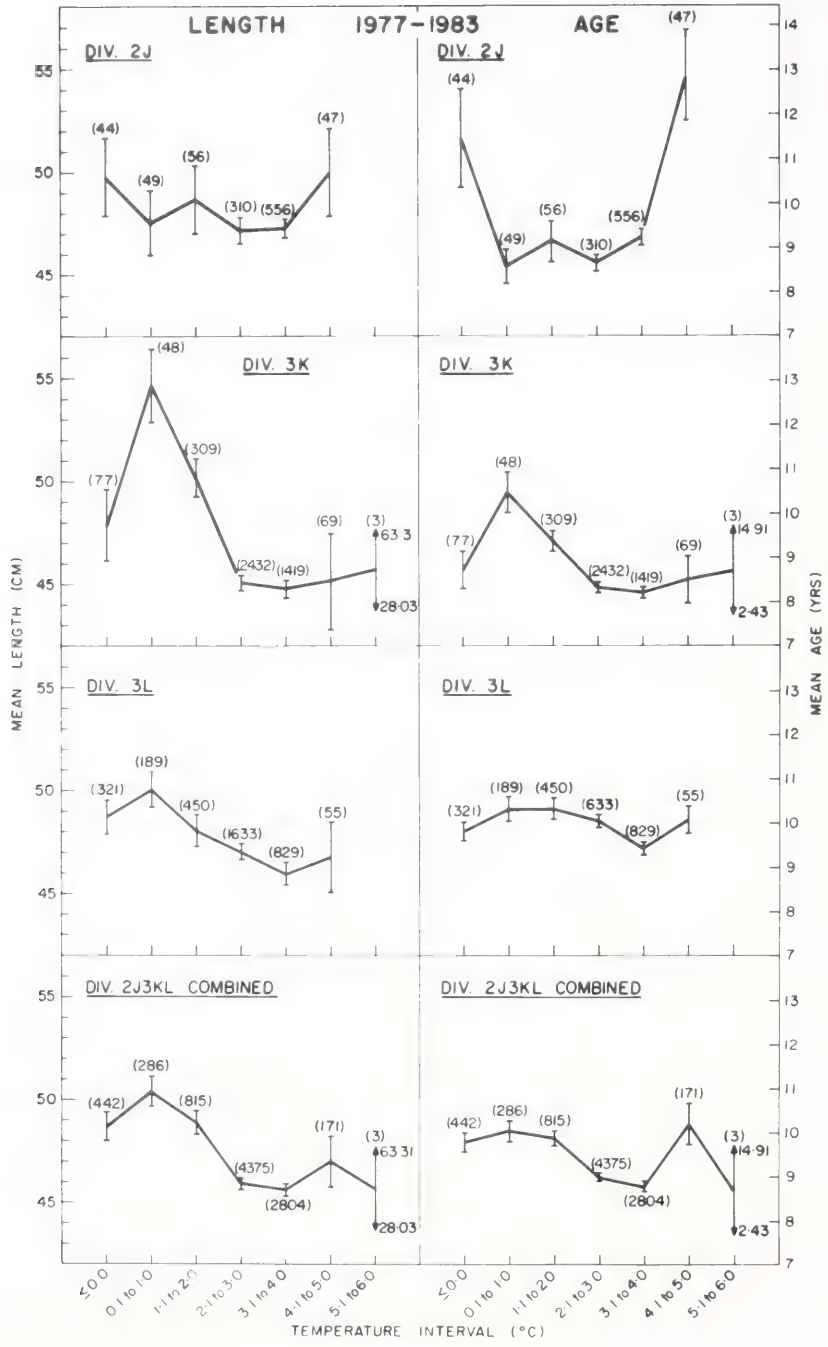

FIGURE 9.—Mean length (cm) and mean age (years) of witch flounder per temperature interval in Div. 2J, 3K, and 3L separately and combined from research vessel surveys during 1977-83. (Number in brackets refers to the number of fish observed.)

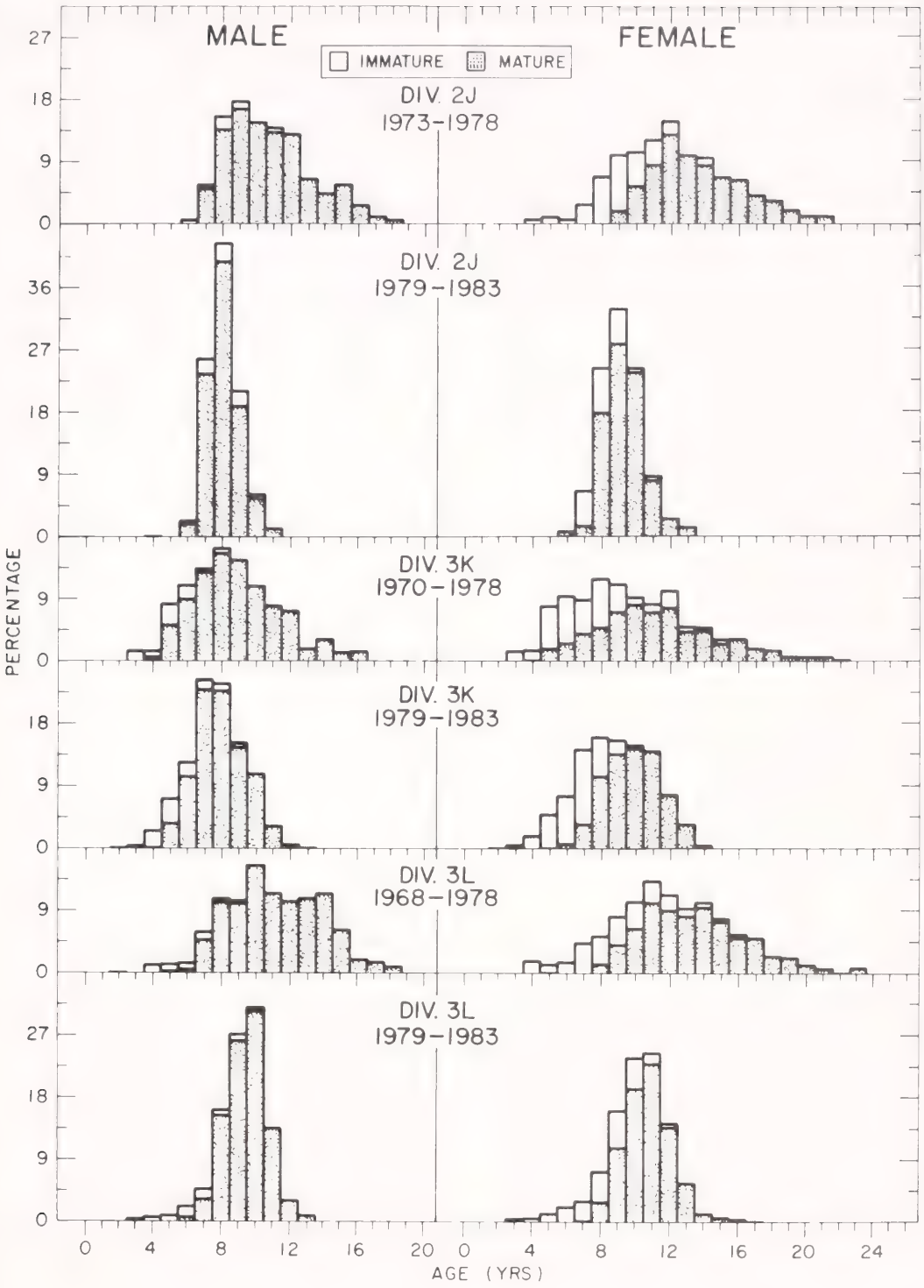

FIGURE 10.—Age compositions of male and female witch flounder in Div. 2J, 3K, and 3L for various time periods between 1968 and 1983. (Shaded areas represent proportions mature at each age.)

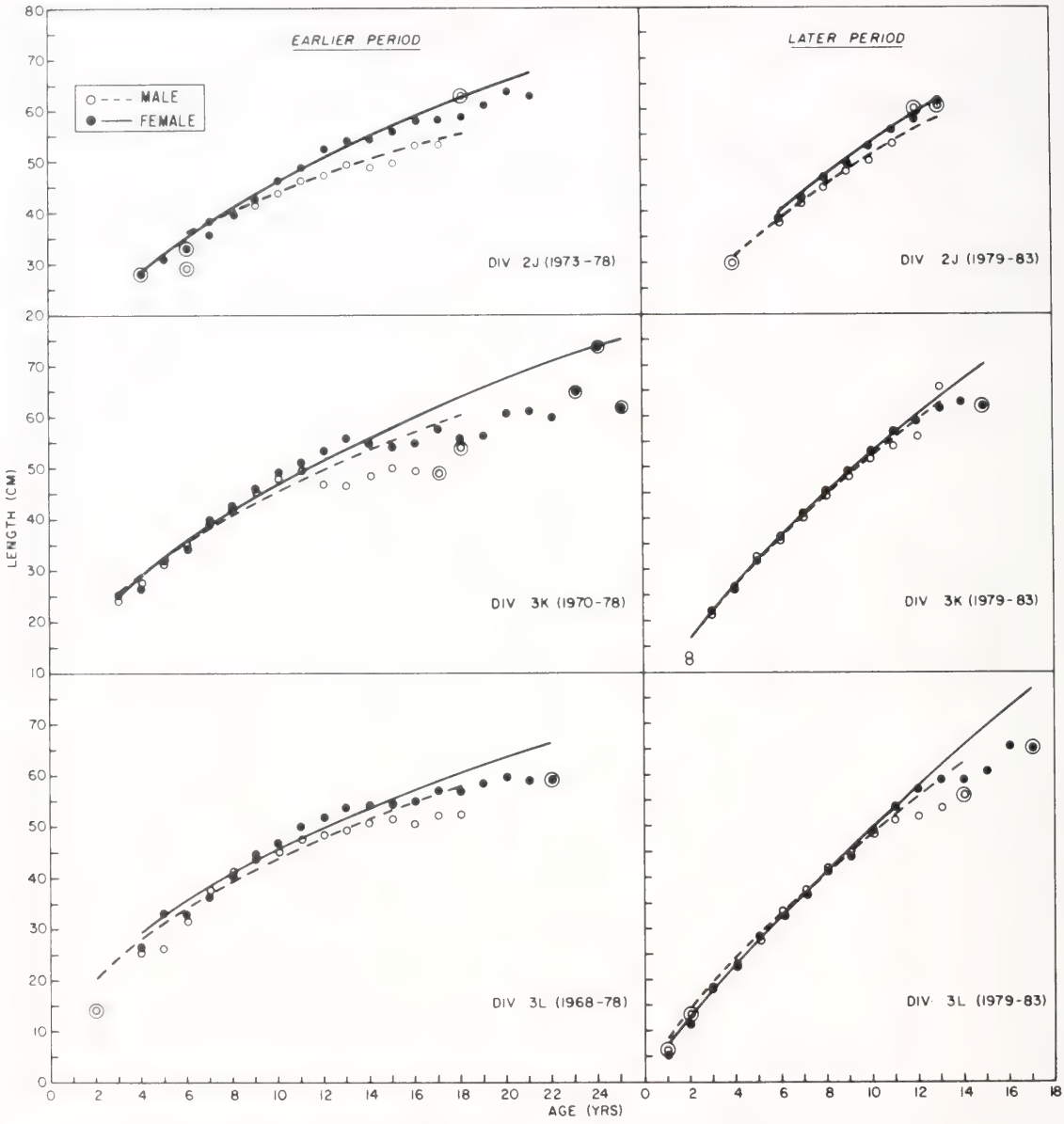

FIGURE 11.—A comparison between two time periods for growth curves of male and female witch flounder in NAFO Div. 2J, 3K, and 3L (circled points indicate only one observation).

(using slopes of the curves as an expression of rate of change of length with age) between the sexes are similar up to about ages 10-12 after which they diverge, particularly if the mean length at age is used as a criterion. While the curves do not appear to fit the mean data points very well in the older ages (and to a much lesser degree the very young ages), the correlation coefficients were all high (Table 1) and all highly significant ($P <$ 0.001). The main reason for this is that the number of observations over age 15 is usually $<1\%$. Taking the 1968-78 males in Div. 3L as an example, even adding a second term to the regression (i.e., c $(\text{Log}_e \text{ Age})^2$) increases the amount of explained variation by $<3\%$. In nearly all cases the mean data points in older ages are below the fitted lines (Fig. 11) suggesting that if observations were more numerous in the older ages, the actual

TABLE 1.—Regressions and correlation coefficients for age and growth ($\log_e$ length (cm) = a + b $\log_e$ age (years)) of male and female witch flounder in NAFO Divisions 2J, 3K and 3L.

Years	Division	Sex	Correlation coefficient (r)	Slope	Intercept
1973-78	2J	Male	0.80	0.40	2.86
		Female	0.89	0.52	2.63
1979-83	2J	Male	0.82	0.54	2.68
		Female	0.81	0.58	2.64
1970-78	3K	Male	0.82	0.48	2.71
		Female	0.88	0.52	2.65
1979-83	3K	Male	0.93	0.71	2.31
		Female	0.96	0.72	2.30
1968-78	3L	Male	0.78	0.48	2.67
		Female	0.80	0.48	2.71
1979-83	3L	Male	0.91	0.75	2.15
		Female	0.94	0.83	1.99

sizes at age are likely to be lower than here calculated. As a result, the predicted size at age is probably only meaningful up to about age 12 for males and age 15 for females for the earlier period, and age 10 for males and age 12 for females in the later period (Fig. 11). Predicted size for males in Div. 3L during the earlier period is also somewhat biased below age 6. Despite these concerns there has been a substantial increase in size at age of both males and females in all three divisions between the earlier periods and later periods (Fig. 12). A comparison of growth curves by division, for each sex and time period (Fig. 13), suggests that the size at age of witch flounder in Div. 3K is higher in all cases than that of Div. 3L. It is also higher than that of Div. 2J in the earlier period; however, in the later period the mean size at age of the younger fish in Div. 2J is generally higher.

Changes in mean size at age in terms of weight are presented in Table 2. With the exception of some of the younger age groups, where there was some small reduction in size at age over the time period, there was a substantial increase in weight at age for all commercial size age groups (age 7+). The amount of increase in weight at age varied (Table 2) among divisions but most age groups had increases in weight between 25 and 62%.

Sexual Maturity

The proportions of mature and immature witch flounder are shown in Figure 10. Most males caught were in a mature condition for all divisions and time periods. Few mature males caught were <6 years old and all were mature beyond 10 years old. The proportions of mature and immature fish at particular ages, however, varied among divisions and time periods. For females, few mature fish were caught <8 years old in most divisions and time periods, with the possible exception of Div. 3K during 1970-78. Most were mature beyond age 12. As with the males, the proportions mature and immature at particular ages varied among divisions and time periods (Fig. 10).

Lengths and ages at M_{50} with 95% fiducial limits are presented in Figure 14. For males there was no significant difference in length at M_{50} for either Div. 3K or 3L between the earlier and later periods (no data for Div. 2J). For females there was no significant change in M_{50} for Div. 3K between the 1970-78 and 1979-83 periods but there were statistically significant reductions in M_{50} from about 47.0 cm in 1973-78 to about 44.2 cm in 1979-83 for Div. 2J and from about 44.8 cm in 1968-78 to 41.5 in 1979-83 for Div. 3L (Fig. 14).

For males there was no significant change in age at M_{50} for Div. 3K between 1970-78 and 1979-83. However, the age at M_{50} for males in Div. 3L was significantly reduced from about 6.0 years in 1968-78 to 3.5 years in 1979-83 (no data available for Div. 2J). For females there was no significant change in age at M_{50} for Div. 3K between 1970-78 and 1979-83. There was a statistically significant reduction in age at M_{50} for Div. 2J from about 10.4 years in 1973-78 to 7.5 years in 1979-83. There was a slight overlap in fiducial limits for Div. 3L, however, for practical purposes the age at M_{50} was reduced from 9.8 years in 1968-78 to 7.8 years in 1979-83.

DISCUSSION

Distribution

Witch flounder are distributed throughout the management zone from the northern slopes of Hamilton Bank to the northern slopes of the Newfoundland Grand Bank. Bowering (1976) suggested that witch flounder reaches its northern limits in the Northwest Atlantic at the northern slopes of Hamilton Bank although catch statistics of NAFO occasionally reported commercial catches north of here. Unpublished data from surveys in Div. 2G and 2H by the Northwest Altantic Fisheries Center, St. John's, Newfoundland have never reported catches of witch flounder in these areas and support the contention of Bowering (1976) and question the accuracy of some commercial catch reports. For the area surveyed, the distribution of witch flounder presented here is

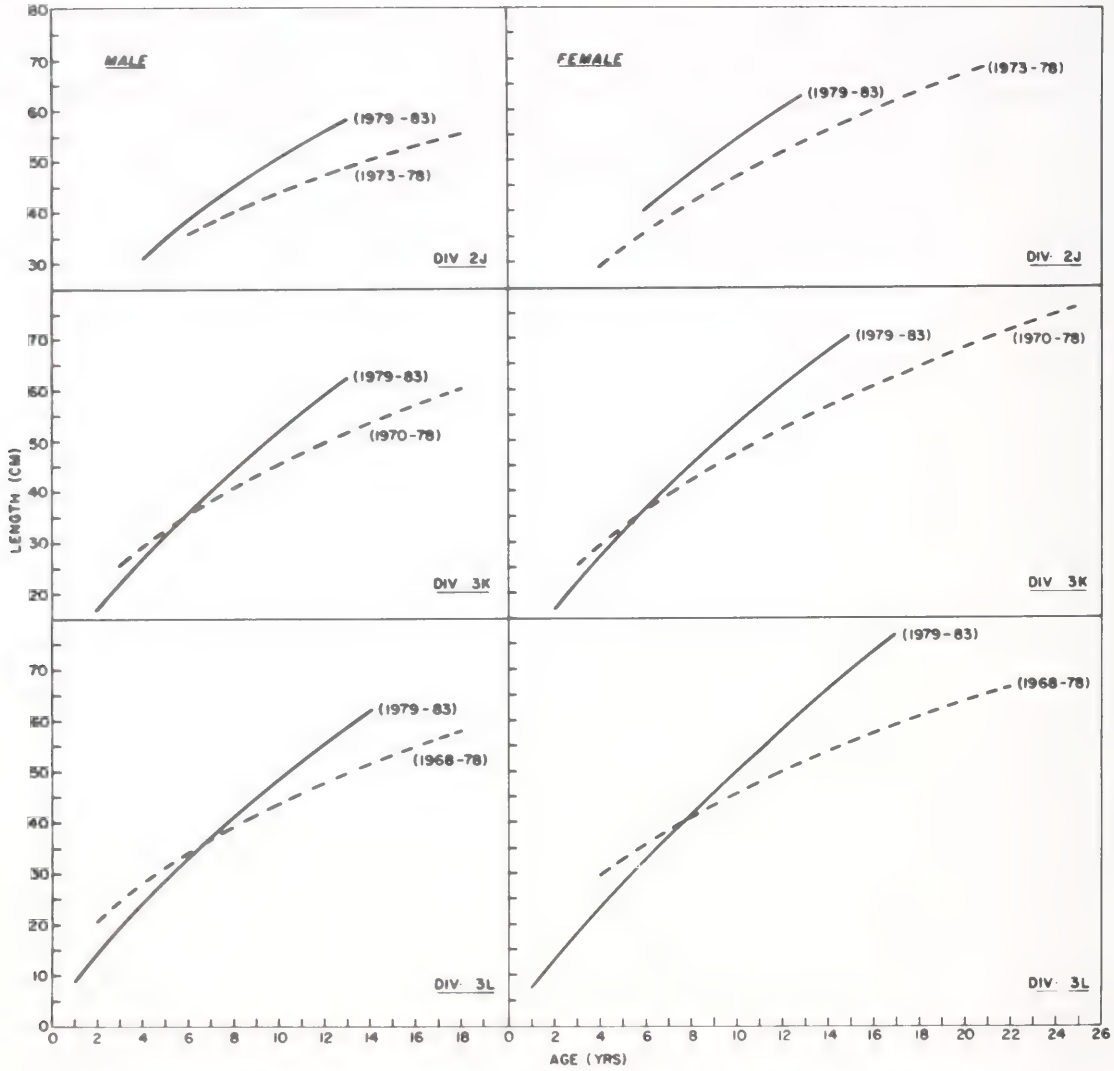

FIGURE 12.—A comparison between male and female witch flounder growth curves in NAFO Div. 2J, 3K, and 3L for earlier and later time periods.

somewhat similar to that published by Bowering (1976) for the 1958-74 period although there was little data available for the southern half of Div. 3K in the Bowering (1976) paper. Although there are no obvious discontinuities in distribution at division boundaries or elsewhere which could account for the occurrence of separate stocks, there are at least three separate stocks of witch flounder reasonably well defined by divisional boundaries as shown by Fairbairn (1981) and Bowering and Misra (1982). This is not to say that some transboundary migrations as adults or through larval drift does not occur when both quite likely do. The largest stock is located in the Div. 3K area according to the catch proportions (Fig. 2) and indices of relative abundance (Fig. 4) presented here. Bowering (1985) reported that minimum trawlable biomass estimates for the management zone during recent years are about 2,500 t, 36,000 t, and 7,800 t for Div. 2J, 3K, and 3L respectively, indicating that the biomass index in Div. 3K is nearly four times higher than Div. 2J and 3L combined.

The major offshore fishing effort towards witch flounder in this zone usually takes place in winter and early spring in areas where prespawning concentrations generally occur, particularly in the

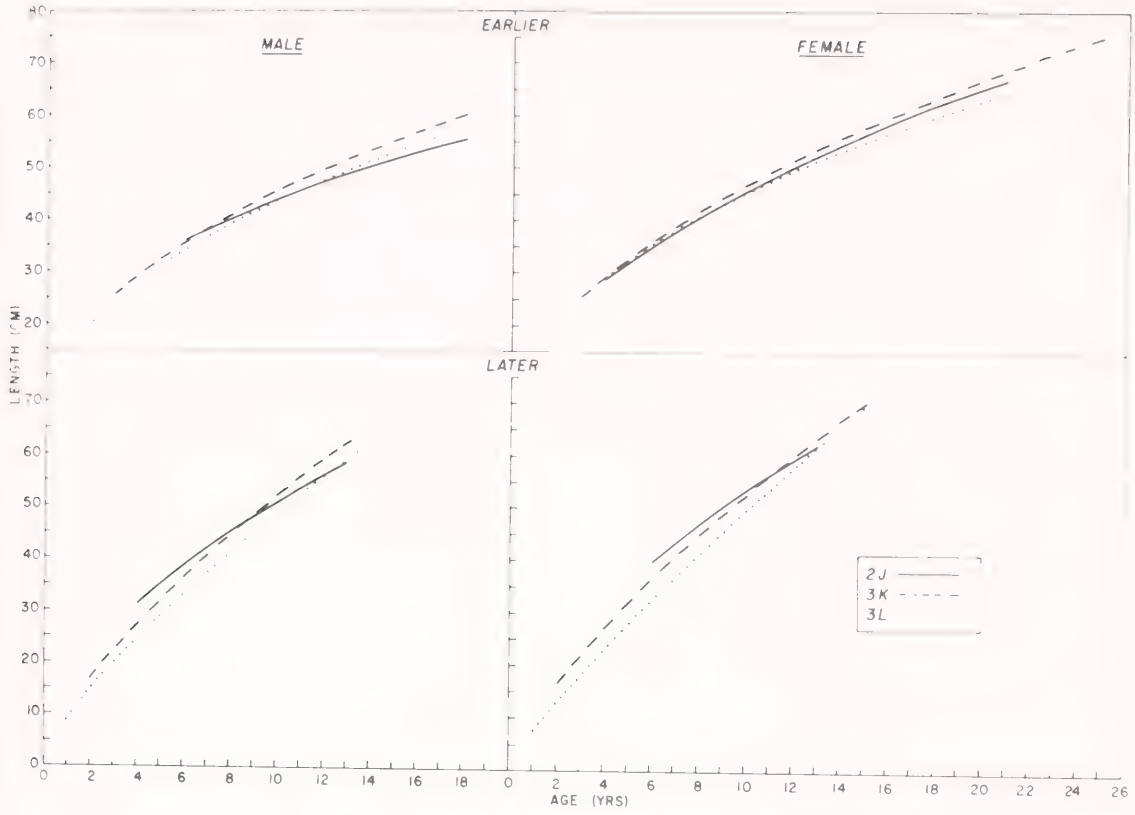

FIGURE 13.—A comparison among divisions for growth curves of male and female witch flounder from earlier and later time periods.

area of Funk Island Deep in Div. 3K (Bowering 1985). In the late 1960's, however, heavy exploitation occurred in the Hawke Channel area of Div. 2J with average annual catches of about 5,000 t as seen in Figure 2. Templeman (1966) reported three research vessel catches of witch flounder in Hawke Channel during April 1963 and 1964 of 2,300 kg, 1,400 kg, and 3,300 kg/hour where these fish appeared to be concentrated. Recent biomass levels of 2,500 t for this area as previously mentioned are now quite low in comparison to the annual catch during the late 1960's even if the catchability coefficient of the survey gear is considerably <1. According to results published in Bowering (1985) the age composition of commercial catches from the management zone in 1976 were as old as 25 years compared to a 15-yr-old maximum in 1984. In 1976, more than 40% of the commercial catch was older than age 12 whereas in 1984 <5% of the catch was older than age 12. It may be that concentrations during prespawning have depleted these stocks, particularly the older, mature fish. This may have contributed to the dramatic decline in landings since the early 1970's. Unfortunately, estimates of biomass for these areas prior to heavy exploitation are not available for comparison.

Witch flounder in this study were not caught deeper than 900 m or at bottom temperatures >7.0°C (higher temperatures were not encountered throughout the study area). Bowering (1976), for the Newfoundland Region as a whole during 1958-74, did not report catches of witch flounder beyond a depth of 869 m, but they were caught at bottom temperatures up to 10°C. Those catches at high temperatures were due mainly to the inclusion of catch data from the southern Grand Bank area (Div. 3N and 3O), where water temperatures are highly influenced by the Gulf Stream. Markle (1975), in studying young witch flounder on the slope off Virginia, caught them down to a depth of 1,408 m and a temperature of 11.3°C. He also found that they were caught in significantly deeper and cooler water in November compared to June. Such a comparison was not possible here. It should be pointed out, however,

TABLE 2.—Changes in mean size at age of witch flounder from 1973-78 to 1979-83 for Division 2J; 1970-78 to 1979-83 for Division 3K; and from 1968-78 to 1979-83 for Division 3L. Only ages common to both periods are included in the comparisons.

	Mean weight (g)				Mean weight (g)		
	Male				Female		
Age (yr)	Early	Late	% Difference	Age (yr)	Early	Late	% Difference
				Division 2J			
6	137.53	363.07	164.0	6	215.90	369.73	71.3
7	368.39	486.10	32.0	7	283.25	522.90	84.6
8	430.66	620.16	44.0	8	410.45	723.18	76.2
9	480.01	781.58	62.8	9	528.07	884.41	67.5
10	579.47	907.10	56.5	10	708.68	1,113.32	57.1
11	708.15	1,128.11	59.3	11	860.30	1,355.22	57.5
12	751.14	1,739.31	131.6	12	1,101.59	1,535.95	39.4
13	882.54	1,842.59	108.8	13	1,211.18	1,885.11	55.6
				Division 3K			
3	71.05	44.58	−37.3	3	84.24	47.46	−43.7
4	112.53	99.48	−11.6	4	102.27	99.48	−2.7
5	178.11	199.25	11.9	5	183.34	193.28	5.4
6	257.01	302.54	17.7	6	252.89	300.23	18.7
7	389.19	425.08	9.2	7	402.56	450.79	12.0
8	492.65	602.41	22.3	8	513.94	633.84	23.3
9	654.76	797.71	21.8	9	660.32	842.68	27.6
10	791.92	1,017.10	28.4	10	869.52	1,116.27	28.4
11	872.61	1,202.60	37.8	11	1,003.37	1,416.30	41.2
12	723.18	1,342.57	85.6	12	1,165.69	1,644.10	41.0
13	714.56	2,340.84	227.6	13	1,362.86	1,889.40	38.6
				14	1,277.29	2,062.18	61.5
				15	1,217.44	1,950.18	60.2
				Division 3L			
4	87.79	58.23	−33.7	4	93.95	59.68	−36.5
5	93.95	119.42	27.1	5	215.90	123.66	−42.7
6	179.51	213.39	18.9	6	208.90	209.79	0.4
7	326.43	324.28	−0.7	7	303.71	316.72	4.3
8	451.56	471.19	4.3	8	429.91	466.03	8.4
9	572.11	617.26	7.9	9	626.00	607.17	−3.0
10	632.86	822.34	29.9	10	729.69	845.70	15.9
11	767.38	990.45	29.1	11	920.52	1,168.74	27.0
12	821.16	1,032.36	25.7	12	1,046.37	1,477.51	41.2
13	870.14	1,151.31	32.3	13	1,196.39	1,632.47	36.4
14	962.30	1,367.11	42.1	14	1,211.96	1,628.61	34.4
				15	1,227.67	1,803.88	46.9
				16	1,265.96	2,362.17	86.6
				17	1,445.34	2,299.83	59.1

that Markle (1975) referred only to fish <5 years old, whereas this study has few fish <5 years old.

Witch flounder preferred depths and temperatures at intermediate levels among these samples in Div. 2J, 3K, and 3L. Preferred depth in Div. 3K is more clearly defined than preferred temperature; this is associated with the occurrence of smaller younger fish at intermediate values of the observed ranges. Powles and Kohler (1970) suggested that juveniles in the Gulf of St. Lawrence were in deeper water, separate from the adult, a built-in conservation mechanism for the young. S. J. Walsh (pers. comm.)[2] on the other hand, in examining the distribution of juvenile versus adult witch flounder in the Gulf of St. Lawrence also found that juveniles (<30 cm) had a well-defined preferred depth range whereas the adults (≥30 cm) were distributed over a much wider depth range. For demersal fish it is more common for younger fish to be found in shallower water with most of the larger fish in deeper water (e.g., See Bowering [1984] for Greenland halibut). There is some indication that young American plaice in the Newfoundland-Labrador area may also occupy some intermediate depth over the

[2]S. J. Walsh, Juvenile Flatfish Biologist, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada, pers. commun. 1986.

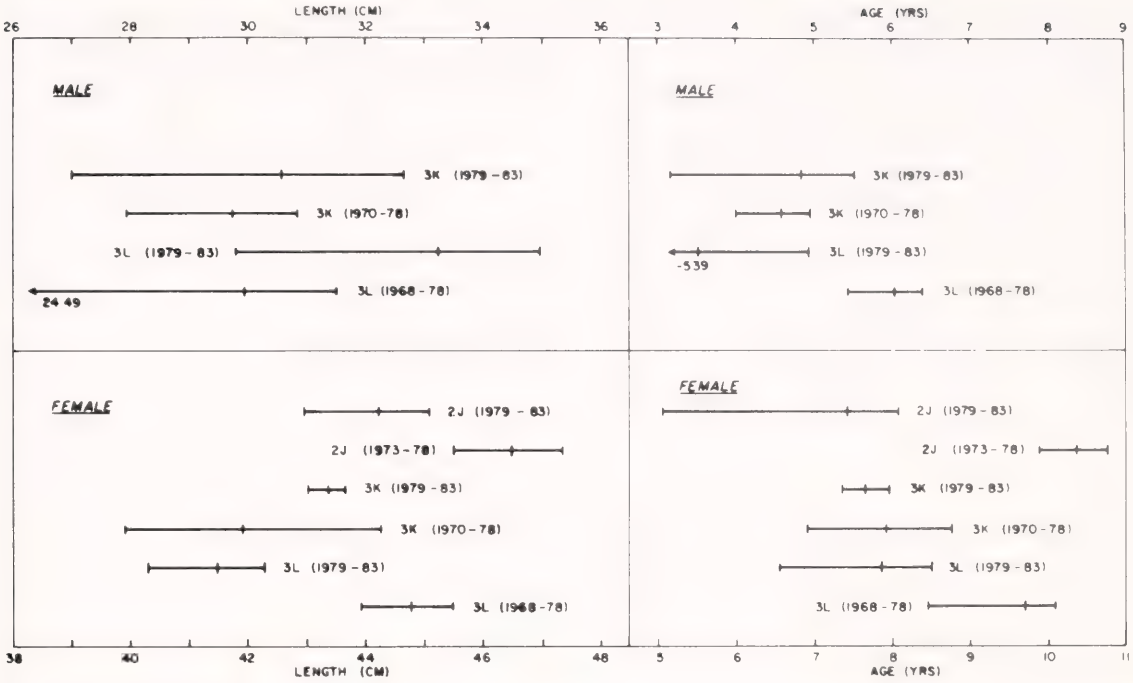

FIGURE 14.—A comparison of lengths (cm) and ages (years) at which 50% of male and female witch flounder are mature from NAFO Div. 2J, 3K, and 3L from earlier and later time periods.

range of its distribution (T. K. Pitt[3]), although the size-depth distribution is not as well defined as presented here for witch flounder. Walsh (1984) concluded, on the other hand, that juvenile plaice occupy the same depth ranges as the adult plaice on the Grand Bank. It should be noted that the results presented in the present paper reflect the depth and temperature preference of young versus old adult witch flounder and not juveniles versus adults as in the studies mentioned.

Age and Growth

The age compositions of witch flounder have changed substantially for all three NAFO Divisions over the study period, with a much shorter life span experienced in recent years. The impact of the reduced life span appears to be greatest on the Div. 2J stock. This may very well be the result of heavy exploitation on prespawning concentrations in the late 1960's when catches were double recent levels of estimated biomass (Bowering 1985). Bowering and Brodie (1984) showed a similar reduction in the life span of witch flounder in the Gulf of St. Lawrence. However, that reduction was more dramatic because it occurred over a shorter time. In 1976, the commercial catches in the Gulf of St. Lawrence comprised fish up to 26 years old compared with a maximum age of 16 years old by 1981. Bowering and Brodie (1984) attributed the sudden change in the population age structure to the fact that almost the entire fishable stock is located in a small area during the winter months when the fishery is most intense. This is particularly true for small stocks such as that in Div. 2J, where it may not be economical to direct effort when the fish are not densely concentrated. In Div. 3K, where the stock biomass is relatively high in comparison to that of Div. 2J and 3L, the fishery is spread more through the year, although the main effort is still directed towards prespawning concentrations. Therefore, the reduction in age groups could be over a longer time period and therefore less dramatic, which seems to be the case here. However, this argument can only be true if, because of such a pattern of fishing, the fishing mortality exerted in areas such as Div. 2J is much higher than for areas such

[3]T. K. Pitt, Section Head, Flatfish Research, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada, pers. commun. 1986.

as Div. 3K. Precise information on fishing mortality is unavailable.

The age composition for the 1970-78 period in Div. 3K indicates that little more than 10% of the population was older than 15 years. However, more than 40% of the commercial otter trawl catches in 1976 by both Canada and Poland in Div. 3K were comprised of fish 15 years and older, and more than 30% were 17 years and older (Bowering and Pitt 1977). Thus the impact of the fishery was greatest on the older age groups, and this could explain the rapidity of the disappearance of the population.

Accompanying the reduced age span was an overall increase in size at age for both sexes in all three divisions. The mean size at age for older fish showed a considerable increase from the earlier to later periods examined, whereas the mean size at age for the younger fish was not very different between the two periods. The substantial increase in size of older, commercially exploited fish may be the result of reduced abundance as indicated by the reduced age span. While there is no direct evidence here of density dependent growth, there have been studies published which show that it does occur. Bowering and Brodie (1984) showed that there was a systematic increase in mean size at age of witch flounder in the Gulf of St. Lawrence from 1976 to 1981 for age groups fully recruited to the commercial fishery accompanied by a significant reduction in the age span of the stock. They suggested it was likely the result of increased exploitation and subsequent reduction in abundance. They also showed that because of the increase in growth rate in particular the stock biomass remained relatively stable despite the fact that the stock abundance had been reduced. Unfortunately, estimates of stock abundance and biomass are not available for the earlier periods of this study for comparison.

Bowering (1976) ruled out temperature as a major contributing factor for changes in growth of witch flounder in the Canadian Northwest Atlantic for two reasons: 1) they mainly inhabit depths that are not usually subjected to wide fluctuations in bottom temperature and 2) the growth rates of witch flounder in the more southerly regions are much slower than in the more northerly regions, the opposite of what one would expect if temperature were considered to have a significant influence on its growth rate. Bowering and Brodie (1984) suggested that given the feeding behaviour of adult witch flounder as described by Rae (1969), competition with other species is unlikely to be a significant factor in changes in growth rate, and within species competition is likely to be a more important factor.

Sexual Maturity

It should be pointed out that immature males are not particularly well sampled by the survey gear, and, therefore, the maturity rates may be slightly biased. However, any bias would be consistent for males in all divisions. On the other hand, although younger females are also not well sampled, the first occurrence of mature fish in the samples is reasonably well established. Most of the data here were collected in late summer and early autumn, several months after spawning, and one could have some concern as to the interpretation of immature versus fully recovered gonad condition. I do not feel, however, that witch flounder in these areas studied present significant cause for concern in this regard. The Greenland halibut, a flatfish whose gonad condition is more difficult to interpret, was sampled from northern Labrador in the autumn for visual interpretation of gonad condition complemented by histological analysis by Walsh and Bowering (1981). They found no significant error in the visual (at sea) interpretation of gonad condition, at least for females.

Due to the time of year when sampling occurred, a slight bias in true size and age and maturity may occur; however, it should be consistent throughout the division and time periods examined. Therefore, comparisons should not be biased. Despite such concerns, for the data presented here, it would appear that there was a significant reduction in both mean length and mean age at 50% maturity for both Div. 2J and 3L females and Div. 3L males (for mean age only) over the study period. For Div. 3K there was no significant change in either mean length or mean age at 50% maturity for either males or females over the time period.

Molander (1925) found that for plaice and flounder in the Baltic, maturity appeared at a lower age but at a higher length with increased growth rate, and suggested that when growth rate was poor, the age at maturity was higher. Pitt (1975) found that for American plaice on the Newfoundland Grand Bank, the faster growing fish matured at an earlier age but at approximately the same size. Bowering and Brodie (1984) found similar results for witch flounder in the Gulf of St. Lawrence. It has been suggested,

therefore, that sexual maturity may be more dependent upon body size than on age; the hormones that stimulate sexual maturity may only be produced when the fish and gonads reach a certain size or stage of development. Such a conclusion would not be reached from the results presented here for Div. 2J and 3L, and there are other exceptions in the literature such as those of Fleming (1960) and Pinhorn (1966) for cod in the Newfoundland and Labrador area. It should be noted, however, that although there are statistically significant reductions in mean sizes at maturity presented here, they may not be biologically significant; the actual relationships between size and age at sexual maturity is still unclear although some physiologists, such as Alm (1959), believe that it is closely related to initial growth rate. Since little is known about the early life history of witch flounder in the Newfoundland-Labrador area, such relationships between maturity, size, and age are difficult to evaluate conclusively.

ACKNOWLEDGMENTS

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EARLY LIFE HISTORY OF SAND LANCE (*AMMODYTES*), WITH EVIDENCE FOR SPAWNING OF *A. DUBIUS* IN FORTUNE BAY, NEWFOUNDLAND

E. L. DALLEY AND G. H. WINTERS[1]

ABSTRACT

Ichthyoplankton surveys in Fortune Bay, Newfoundland, indicate that sand lance (Ammodytes sp.) larvae occur annually in Fortune Bay from February, when recently hatched yolk-sac larvae occur, until July/August when, it is assumed, the larvae have grown to the size of metamorphosis and have taken up a demersal existence. Length-frequency data indicate the spawning season to extend from December to May-June, and this extended spawning season probably accounts for the consistent polymodality in length-frequency distribution of sand lance larvae from the Newfoundland area.

Meristic development is shown to be complete by the time a length of 35-40 mm is reached and analyses of meristic counts indicate that the large (>20 mm) sand lance larvae caught in Fortune Bay belonged to the offshore species *Ammodytes dubius*. Further, analyses of pre-anal melanophore counts and oceanographic features of the area indicate that yolk-sac larvae taken in Fortune Bay in February were also *A. dubius*. This is the first record of the occurrence and spawning of *A. dubius* in coastal Newfoundland waters. This finding is significant in view of the current confusion regarding the appropriate taxonomy of sand lance populations in the Northwest Atlantic.

Sand lance, *Ammodytes* sp., are widely distributed in the Northwest Atlantic from Greenland south to Cape Hatteras, NC (Liem and Scott 1966). Although presently commercially unimportant, they hold a strategic niche as a major food organism for numerous commercial fish species, and Winters (1981, 1983) listed sand lance as a prey of haddock, Atlantic cod, silver hake, yellowtail flounder, American plaice, and Atlantic salmon. They are also fed heavily upon by certain large marine mammals (Overholtz and Nicolas 1979), and it has been postulated (Winters 1983) that their importance as a prey species is enhanced during times of low capelin abundance.

Taxonomy of the Northwest Atlantic sand lance has received considerable attention (Richards et al. 1963; Richards 1982; Scott 1968, 1972; Winters 1970). Generally two species are recognized in the Northwest Atlantic, i.e., *Ammodytes americanus* (=*Ammodytes hexapterus*), which is the deep-bodied, inshore form, and *Ammodytes dubius*, the slender-bodied, offshore form. Their taxonomy, generally, is confused by the presence of two clines in their meristic character frequencies: one north to south cline, the other inshore to offshore cline, with frequent overlap in the ranges of meristic numbers (Reay 1970). The validity of the two species is also questioned due to correlations of meristic numbers with environmental conditions (Scott 1972). In the Newfoundland area, however, the two species exhibit quite distinct meristic counts (Winters 1970). For the purposes of this paper we use the species classification of Liem and Scott (1966).

Winters (1970) has described the meristics and morphometrics of both species from the Newfoundland area and described *A. dubius* in the offshore and *A. americanus* inshore. Winters (1981, 1983) has described aspects of the biology of *A. dubius* from the Newfoundland Grand Banks. Little information exists on their early life history in the Newfoundland area. Dannevig (1918) provided length and distribution information for 89 specimens of sand lance captured off southern Newfoundland in surface and vertical hauls in early summer 1915. He assigned the specimens to *A. tobianus* (Linnaeus), a European inshore species. Frost (1938) presented information on the distribution of sand lance larvae around Newfoundland from 1931 to 1935. No size information was provided, and she assigned all the specimens from both near shore and the edge of the Grand Banks to *A. americanus*. In spite of its importance as a forage fish to commercially important species, no other information exists for sand lance larvae from the Newfoundland area.

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Information in the literature supports the hypothesis that the two species are allopatric. Winters (1970) found, based on adult samples, that *A. dubius* occurred exclusively in offshore areas and *A. americanus* exclusively in inshore bays around Newfoundland. Reay (1970) pointed out that *A. dubius* is exclusively an offshore species although Richards (1982) indicated that there are offshore components to *A. americanus* in the New England area. This paper presents information on sand lance in Fortune Bay, Newfoundland, as a further test of the hypothesis that the two species are allopatric. Size and distribution (seasonal and diurnal) information on *Ammodytes* larvae both within and at the mouth of Fortune Bay is presented as well as length-frequency information for other parts of the Newfoundland-Labrador area. The development of the definitive number of meristic characteristics is examined to identify the Fortune Bay larvae and, in conjunction with this, aspects of the developmental biology of *Ammodytes* sp. in the area are also described.

MATERIALS AND METHODS

Fortune Bay is a three still fjord located on the south coast of Newfoundland (Figs. 1, 2). Typically it has a two-layered structure with relatively warm (1.9°C) deep water in the outer portion in winter and cold (−0.25°-0.50°C) deep water in summer (de Young 1983). Annual surface temperatures typically range from 0.0°-1.0°C in February to 12°-16°C in August and September.

From June 1979 to February 1981, several ichthyoplankton surveys were carried out annually in Fortune Bay. The target species for the surveys was herring, *Clupea harengus*, but due to low numbers of herring larvae during the first three years the study was relocated, and during 1982-83 only one survey (July) was carried out in each year in Fortune Bay. Sand lance data examined here were collected during these surveys (1979-83).

Larvae collected in 1979-80 were taken by standard oblique plankton tows (Smith and Richardson 1977) using a 60 cm diameter bongo frame with 333 μm mesh netting on one side of the frame and 505 μm on the other. Tows were to a maximum depth of 200 m where possible. Nets were payed out at a speed of 0.77 m/second and retrieved at a speed of 0.38 m/second. After 1980 samples were caught in nets when both sides of the bongos were equipped with 333 μm netting.

In February 1981, collections were made using stepped oblique tows (5 minutes at each of 200, 150, 100, 50, 20, and 0 m) with a nonclosing N.I.O. rectangular midwater trawl (RMT-8) (Baker et al. 1973). During this survey all stations were fished during 6 hours of daylight with sets on the same stations being repeated after dark. A 10-min surface tow (3/4 m conical plankton net, 333 μm mesh) was carried out during each of the oblique tows with the RMT-8.

In June 1981, sand lance larvae were collected using bongo nets during the regular survey and also from special stations to investigate diurnal distribution. During each of these special stations, bongos were fished obliquely (to 200 m), and 3/4 m conical plankton nets (333 μm) were fished for 10 minutes at the surface during daylight hours and again (at the same positions) after dark of the same day.

Catches from all trips were preserved in a 5% formalin solution buffered with sodium borate. Fish larvae were later sorted, identified, counted, and measured. Total length was recorded to the nearest millimeter. A Macdonald and Pitcher (1979) mixture analysis was performed on the length-frequency distribution of the large sample from June 1979 to investigate the fit of the data to mixtures of normal distributions approximating the data.

Species designation was determined using meristic characters where possible (June 1979, June 1981), namely, vertebral, anal fin ray, and dorsal fin ray counts. Due to their small size, the specimens were stained for cartilage using Alcian blue and counterstained with alizarin red (Dingerkus and Uhler 1977). Counts were then done under a dissecting microscope (20-40× magnification) with the aid of the camera lucida.

Additional sand lance length-frequency data are presented, which have been on file at the Science Branch, Northwest Atlantic Fisheries Center in St. John's. These sand lance were collected incidentally during tows for other target species around Newfoundland using fishing and plankton gear (see Figures 1 and 4).

RESULTS

Seasonal and Diurnal Distribution

Table 1 lists the cruises in Fortune Bay from 1979 to 1983.

Sand lance larvae were encountered during 9 of the 17 cruises in Fortune Bay from 1979 to 1983

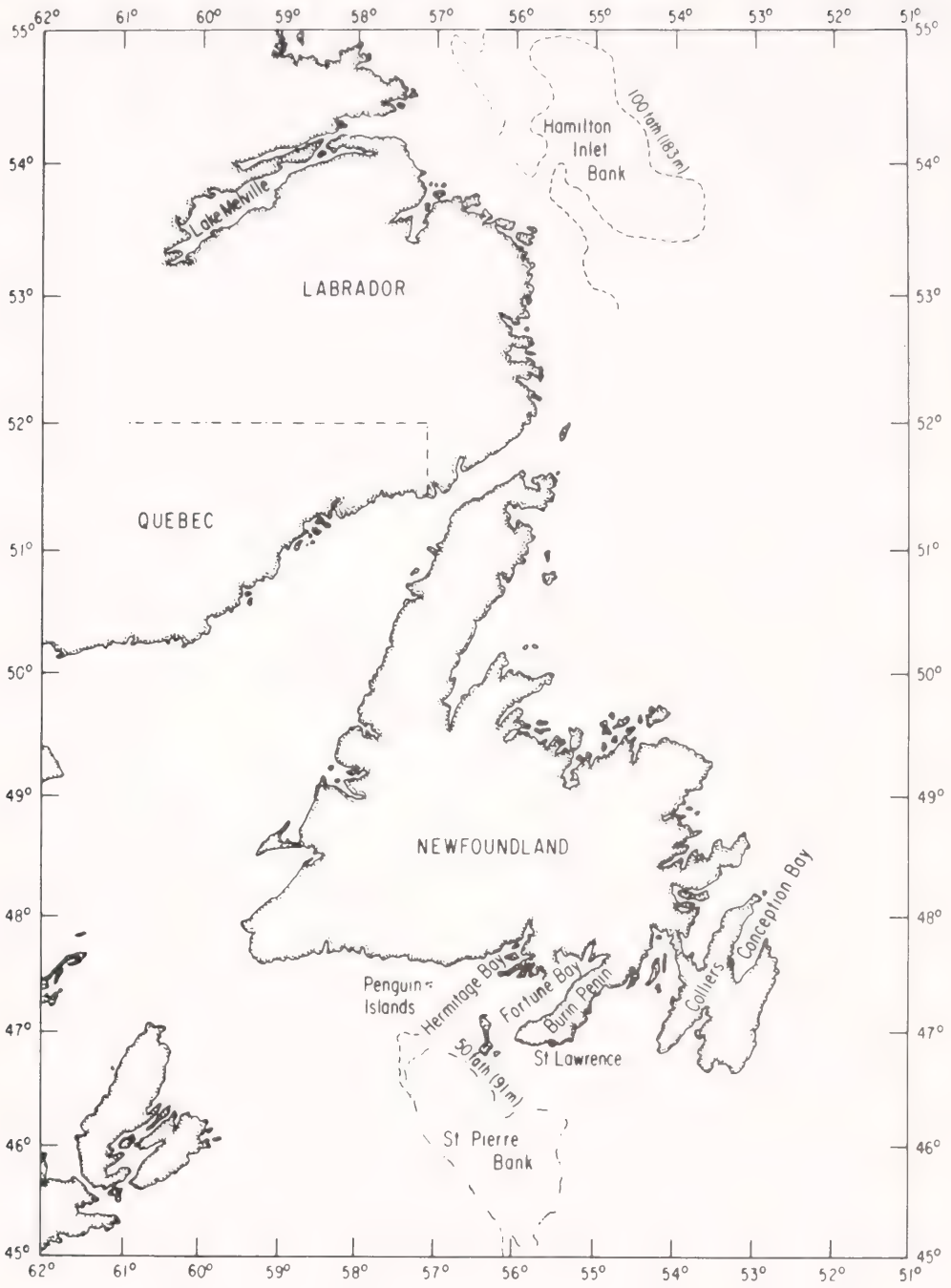

FIGURE 1.—Map of Newfoundland indicating places referred to in the text.

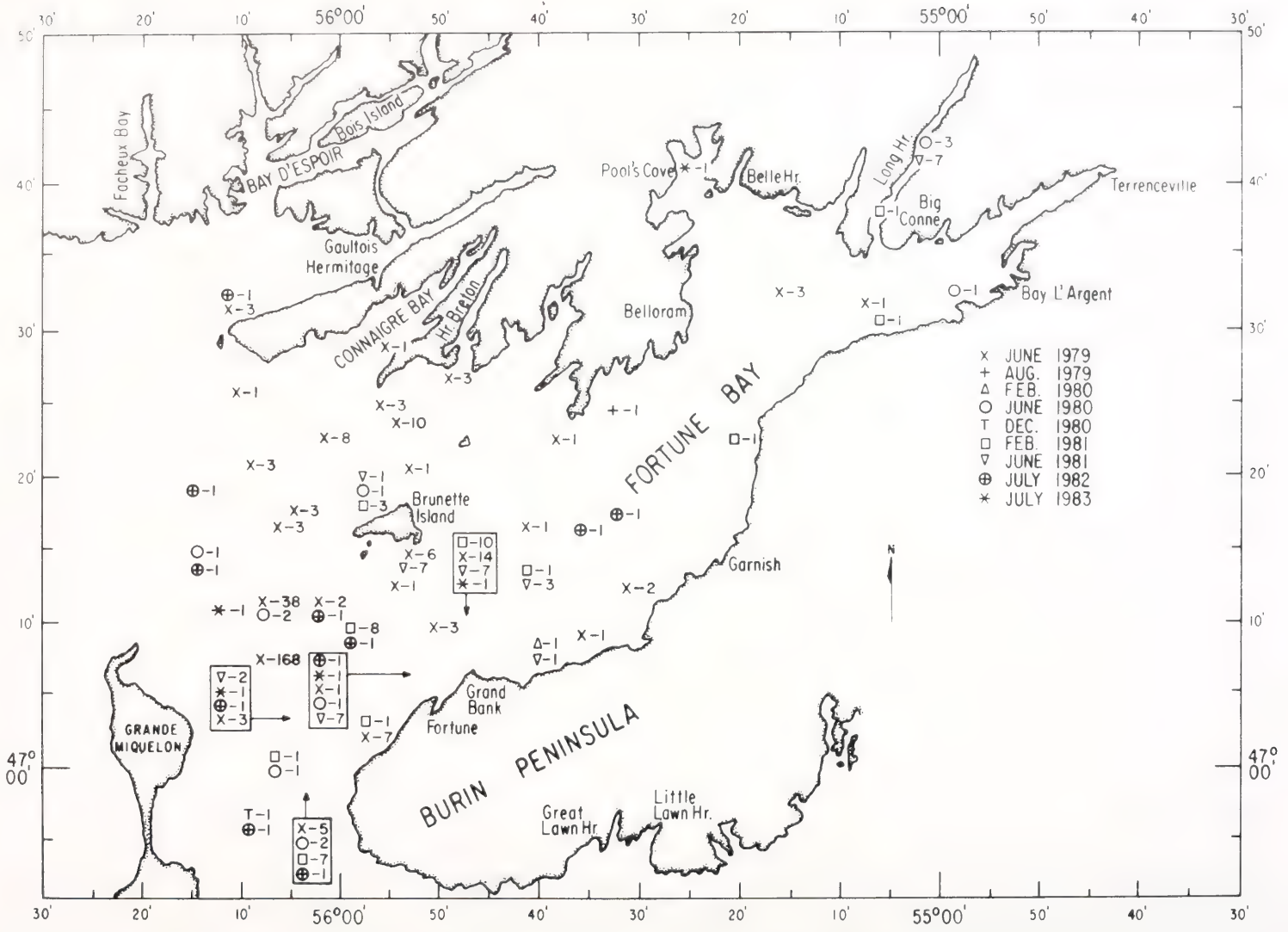

FIGURE 2.—Distribution and catch of *Ammodytes* larvae collected during ichthyoplankton surveys in Fortune Bay from 1979 to 1983.

(Table 1), and the spatial distribution of these catches is shown in Figure 2. Sand lance larvae have a fairly wide distribution within and at the mouth of Fortune Bay; however, the incidence of positive catches and the size of the catches were greatest in the area between Miquelon and Fortune, north to Brunette Island.

The highest and most consistent catches of sand lance larvae were made in June and July, and only two specimens were caught in the August-November period. Yolk-sac larvae were taken only in surveys carried out in February, but larger larvae apparently remained in the water column until July-August at which time it is assumed that metamorphosis is complete, and the postlarvae take on a demersal existence. Macer (1966) gave the length of metamorphosis as 30-40 mm. Surveys in August of 3 consecutive years caught only one larva (43 mm), and surveys later than August caught only a single 82 mm postlarva in December 1980.

Catches of sand lance larvae from two periods in 1981 illustrate day-night variability in catches, especially at the surface (Table 2). During February, 44 stations were fished twice the same day, once during daylight and once after dark using stepped-oblique tows with the RMT-8 and surface tows with conical nets. Thirty-two larvae (94%) (mean length of 7.7 mm) were taken in night sets: 2 in oblique tows and 30 in surface tows. Of the two caught during daylight hours, one was in the surface tow and one in the oblique.

In June, 12 stations were fished using standard oblique tows with bongo nets and horizontal surface tows with conical nets during daylight and darkness of the same day. Twenty-five larvae

TABLE 1.—List of ichthyoplankton surveys carried out in Fortune Bay, Newfoundland, 1979-83, indicating gear fished, number of stations, numbers, and length information of *Ammodytes* sp. caught.

Cruise	Date	Gear[1]	No. stations fished during survey	No. positive sets	No. larvae caught	No. extra sets	No. positive catches (extra sets)	No. larvae in extra sets	Length range (mm) (all larvae)	Mean and SD of total length (mm)
Marinus 15	June 1979	B	71	28	302				10-43	22.9 (15.7)
Shamook 51	Aug. 1979	B	60	1	1					43.0
Marinus 21	Nov.-Dec. 1979	B	53							
Shamook 57	Feb. 1980	B, R	25, 25	1	1				8.0	
Marinus 25	June 1980	B	52	8	12				8-40	18.3 (9.5)
Marinus 28	Aug. 1980	B	42							
Shamook 64	Sept. 1980	R	50							
Shamook 67	Nov. 1980	B	48							
Shamook 69	Dec. 1980	B	52	1	1	[2]28B,28S				82.0
Shamook 71	Feb. 1981	R, S	44, 44	12	34				6-12	7.7 (1.0)
Shamook 76	June 1981	B	52	4	8	[2]24B,24S	8	27	12-61	38.4 (14.2)
Marinus 39	Aug. 1981	B	52			[2]22B,20R				
Shamook 79	Oct. 1981	B	52							
Shamook 81	Dec. 1981	R	35							
Shamook 82	Feb. 1981	R	29							
Shamook 88(2)	July 1982	B	52	11	11				14-46	22.1 (10.4)
Shamook 98(2)	July 1983	B	52	5	5				11-22	14.8 (4.2)

[1]B = BONGO, R = RMT-8, S = Surface net.
[2]Half of sets with each gear type during daylight; half at same station during darkness of same day.

TABLE 2.—Numbers of sand lance larvae caught in oblique[1] and surface tows during investigations into day-night catch variability, February-June 1981.

	Day				Night			
	February		June		February		June	
Type of tow	Oblique	Surface	Oblique	Surface	Oblique	Surface	Oblique	Surface
No. of sets	44	44	12	12	44	44	12	12
No. of positive catches	1	1	1	0	2	8	3	4
No. of Ammodytes larvae caught	1	1	2	0	2	30	9	16

[1]Oblique tow with RMT-8 in February, bongo in June
[2]Includes 1 set at dusk in which 6 larvae were captured.

(93%) of 27 were taken in night sets: 16 at the surface and 9 in oblique tows. Two were caught in the oblique tows, and none, at the surface during daylight.

Size and Length-Frequency Distributions

Mean length data (Table 1) illustrate the annual variation in mean size during the late June-July period. In 1979, 1980, and 1982, the mean lengths of sand lance were 22.9 mm, 18.3 mm, and 22.1 mm, repectively. The 34 larvae caught in June 1981 were larger with a mean length of 38.4 mm, and the 5 caught in early July 1983 were smaller with a mean length of 14.8 mm.

Length-frequency distribution of the largest samples from Fortune Bay are shown in Figure 3. The distributions from June of each year indicate a wide range of lengths, and although samples from June of 1980 and 1981 are not large, the extended range in both suggests that the distribution is not unimodal and that there is more than one spawning cohort present. This extended length range may also result from delayed hatching or a combination of both these processes. In June 1979 there is a distinct mode at 23 mm with others probable at 14-15 mm and another at 29 mm. The length frequency of the June 1979 sample was subjected to modal analysis as described by MacDonald and Pitcher (1979). Three modes were interpreted from the length-frequency histogram. The results of the analysis indicated normal distributions with means at 13.4, 22.2, and 28.8 mm with standard deviations of 1.76, 3.02, and 4.36 mm, respectively (Table 3). The June 1981 sample of 33 larvae has a distinct mode at 45 mm, which is widely separated from a group of fish ranging in length from 12 to 17 mm. The wide range and polymodality in the length distributions of the June samples is good evidence of multiple spawning cohorts although differential hatching rates of the same cohort cannot be ruled out (S. Richards[2]). Given that sand lance larvae take 3-5 months (Reay 1970) to attain metamorphic sizes (30-40 mm, Macer 1966), the above observations suggest a spawning season extending from December through to April. In addition, the occurrence of larvae as small as 11 mm in July and 8 mm in June 1980 (Table 1) suggests that spawning may occur as late as May or June in certain years.

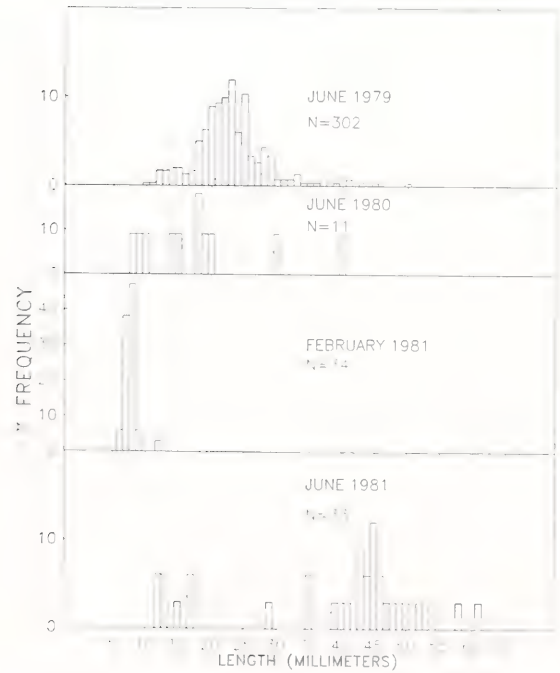

FIGURE 3.—Length-frequency distributions from Fortune Bay sand lance samples.

TABLE 3.—Results of the MacDonald and Pitcher (1979) method of analyzing length distribution mixtures of sand lance, June 1979, assuming a mixture of three (spawning) components. Results assuming only one component are also shown.

	Component	Percent of total population in component (SE)	Mean length (SE)	Standard deviation (SE)
$K = 3$	1	8.2 (2.9)	13.4 (0.77)	1.76 (0.52)
$\chi^2 = 25.32$	2	78.1 (28.2)	22.2 (0.65)	3.02 (0.53)
df 19				
$P = 0.1504$	3	13.7 (27.1)	28.8 (9.2)	4.36 (3.46)
$K = 1$				
$\chi^2 = 49.55$	1	100	22.4 (0.27)	4.65 (0.19)
df 25				
$P = 0.0024$				

This tendency for protracted length ranges is also evident in the historical samples collected around Newfoundland (Fig. 4). Samples are small, but the two from Labrador range in length from 22 to 55 mm with a break between the larger and smaller groups. The 14 fish from Colliers Bay, Conception Bay exhibit a protracted length range from 28 to 65 mm. The two samples collected off southern Newfoundland (Penguin Is-

[2]Sarah W. Richards, Little Harbor Laboratory, Inc., 69 Andrews Road, Guilford, CT 06437, pers. commun. October 1986.

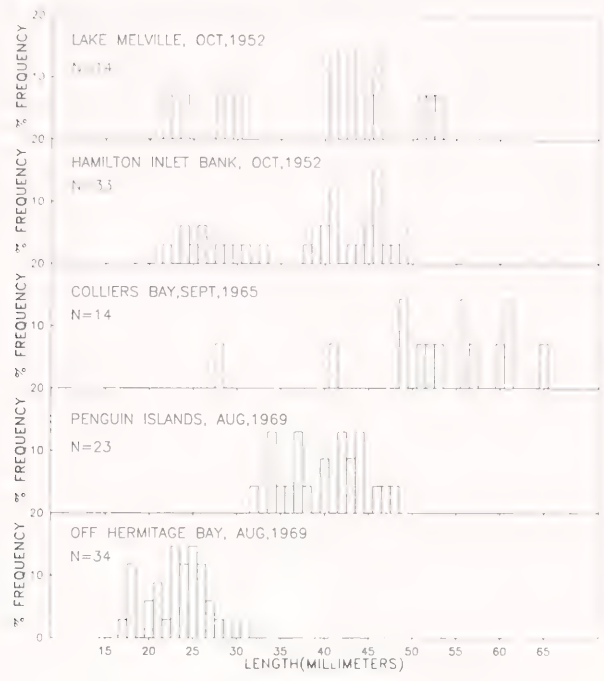

FIGURE 4.—Length-frequency distributions of historical sand lance samples from the Newfoundland area.

lands and Hermitage Bay) (Fig. 1) are interesting because although they were collected approximately 30 miles apart on successive days, the two samples have completely distinct length-frequency distributions. The sample collected on August 20 ranges in length from 32 to 48 mm, and the one collected on August 21 ranges from 17 to 31 mm. The distribution of both of these samples indicates that there may be more than one mode in each of the smaller and larger groups. These two completely different distributions may reflect multiple spawning cohorts or different spawning seasons in the case that they are comprised of different species.

Meristic Development

The staining procedure resulted in cartilaginous tissue being stained blue and ossified tissues red. Very few of the larvae had vertebral columns that stained for both cartilage and bone. The procedure resulted in three categories of vertebral columns. In the first category, the whole column stained blue, and this sometimes made counts difficult because parts of the notochord had not been replaced by individual vertebrae. The second category contained larvae in which part of the vertebral column was stained blue and part was stained red. These were few and had varying portions of red and blue stain. Neither the anterior nor the posterior portion of the vertebral column consistently ossified first. The third category contained those larvae in which all of the vertebral columns were ossified and stained red. Most larvae fell into this category. The observation that larvae in the second category did not show a consistent sequence of ossification may be an artifact of the preservation. Fixation of any protein or its amino acid derivatives will be followed by a drop in pH wherever formaldehyde is employed (Steedman 1976). Low pH causes decalcification or solubility of small deposits of calcium carbonate (Steedman and Omari 1976) and could therefore bias the interpretation of the normal developmental sequence of ossification. Moser (1972), Fritzsche and Johnson (1980), and Matarese et al. (1980) found that ossification of the vertebral column proceeded posteriorly in rockfish, white perch, striped bass, and Pacific tomcod, respectively. The sequence of development and ossification of fin rays was from anterior to posterior and from proximal to distal portions of the rays.

Table 4 and Figure 5 show the vertebral, dorsal fin ray, and anal fin ray counts for the length classes within the samples. The counts include both cartilageous and ossified fin rays. The full complement of dorsal fin rays is not developed until the larvae have attained a size of approximately 40 mm. The full complement of anal fin rays were developed by a size of 35-40 mm total length. Richards (1982) stated that fin ray development varied greatly in 21 specimens of both species but first appeared at 12-13 mm and was completely developed in 23 mm larvae of *A. americanus*. Fin rays first appeared at 14-15 mm in *A. dubius*, but the full complement was not present until after the larvae were greater than 25 mm total length. Scott (1972) found that the definitive number of anal fin rays were attained at a later stage in growth than 30 mm and that the definitive number of dorsal fin rays was attained at about 30 mm for Scotian Shelf *A. dubius*.

Figure 5 indicates that the definitive number of vertebrae is achieved by a total length of approximately 20 mm. As mentioned above, at sizes smaller than this, the notochord had not been replaced by vertebrae. This resulted in clear regions along the column. It was not possible to count myomeres because the staining process resulted in the fleshy parts of the body being cleared.

Matarese et al. (1980) pointed out that considerable variation occurs in the development of meristic structures of Pacific tomcod, *Microgadus proximus*, because the size at which bone ossifies varies from specimen to specimen. Figure 5 illustrates this variation in the mean counts of dorsal and anal fin rays at the smaller length classes.

Species Identification

Sand lance larvae collected in Fortune Bay in June 1979 had a mean vertebral count of 73.98 (SD = 1.66) (Table 4, Fig. 5). From Figure 5 and Table 4, the definitive number of dorsal fin rays varies from 64 to 68 with a mean of 65.53, and similarly the definitive number of anal fin rays varies from 32 to 36 with a mean of 34.09 (Table

TABLE 4.—Results of vertebral, dorsal fin ray, and anal fin ray counts for the length classes of sand lance.

Length class	*N*	Range	Standard deviation	Mean
Vertebrae				
22.5	49	72-76	0.90	73.98
27.5	75	71-76	1.14	73.95
32.5	19	73-77	1.10	74.11
37.5	8	73-75	0.76	74.00
42.5	13	72-75	1.09	73.77
47.5	5	73-77	1.67	74.40
52.5	4	72-75	1.26	73.75
·22.5	173	71-77	1.66	73.98
Dorsal fin rays				
22.5	69	22-45	3.66	30.04
27.5	69	28-47	3.93	35.72
32.5	16	39-65	9.27	49.31
37.5	5	44-66	9.63	61.20
42.5	10	64-68	1.27	65.50
47.5	5	65-67	1.10	65.80
52.5	4	64-67	1.26	65.25
·42.5	19	64-68	1.17	65.53
Anal fin rays				
22.5	67	25-33	1.79	30.66
27.5	72	27-35	1.20	32.17
32.5	18	31-35	1.13	32.89
37.5	6	33-36	1.17	34.17
42.5	8	33-36	1.06	34.38
47.5	4	33-35	0.96	34.25
52.5	4	32-34	0.96	33.25
·37.5	22	32-36	1.06	34.09

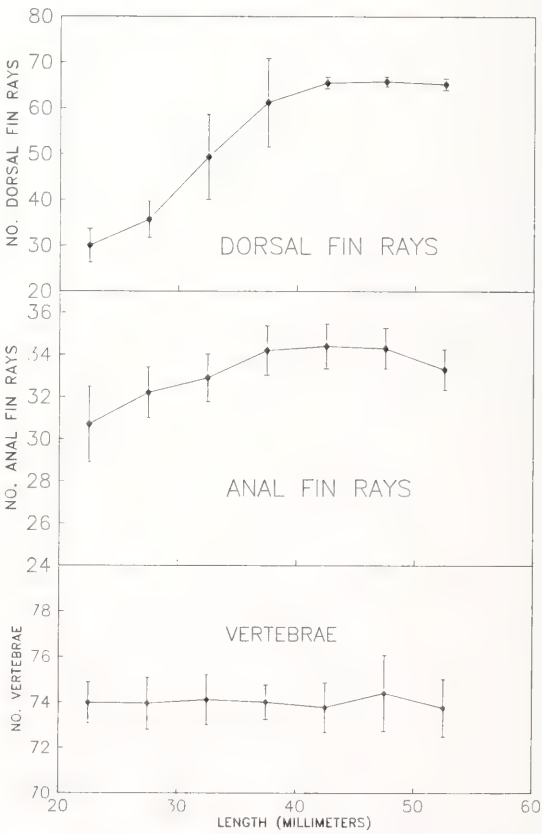

FIGURE 5.—Development of definitive number of dorsal fin rays, anal fin rays, and vertebrae with increasing size of sand lance, showing mean and standard deviation for each length class.

4). Winters (1970) gave mean vertebral counts of approximately 73.8-73.9, mean dorsal fin ray counts of 64.3-64.6, and mean anal fin ray counts of 33.2-33.6 for *A. dubius* from the Newfoundland Grand Banks. Comparable values for *A. americanus* from inshore areas of Newfoundland are 66.2-68.2, 55.7-57.8, and 27.8-30.6. We conclude, therefore, that the larger larvae collected in Fortune Bay in June 1979 belong to the offshore form, *A. dubius*.

The small larvae from February 1981 (lengths 6-12 mm) were examined for the presence of lateral or pre-anal melanophores. Counts of other melanophores (e.g., pectoral and subdorsal) were not possible, due either to the early stage of development of the larvae or to bleaching by the preservative. According to Richards (1982), counts of pre-anal melanophores can be used to distinguish between the larvae of *A. dubius* and *A. americanus*. From 6.0 to 8.9 mm in length, *A. americanus* has 0-16 pre-anal melanophores, and *A. dubius* has 10-21. Full or partial counts were possible for 11 of the larvae. Ten were 6-7 mm in length. Of these, two had 15 pre-anal melanophores, four had 16, one had 17, one had 18, and two had 20. One 9 mm larva had 15 pre-anal melanophores. According to Richards' (1982) criteria, four larvae are definately *A. dubius* because the counts are out of range for *A. americanus*. The other seven are in the upper extreme of the overlap range for the two species suggesting that these too are *A. dubius*. Thus, not only do larger larvae of the offshore species occupy Fortune Bay, but yolk-sac larvae are also present. This suggests that spawning of the offshore species occurs within the bay.

Because *A. dubius* is present on St. Pierre Bank (Winters 1970), we have considered the possibility that the yolk-sac larvae collected from Fortune Bay in February 1981 were transported from St. Pierre Bank. Smigielski et al. (1984) gave times for yolk-sac absorption from 5 to 14 days, depending on temperature. Using minimum and maximum speeds (0.05-0.20 ms^{-1}) of the Labrador Current along the south coast of Newfoundland (Petrie and Anderson 1983), it would take yolk-sac larvae 9-36 days to be carried from St. Pierre Bank to inner stations in Fortune Bay where they were collected. De Young (1983), however, described a seasonal cycle of water exchange for Fortune Bay in which the flow of Labrador Current water over St. Pierre sill (between Miquelon and the tip of the Burin Peninsula (Fig. 2)) is minimal in winter months and predominates in the summer. Under normal current conditions, it appears unlikely that these yolk-sac larvae were transported over St. Pierre Bank into Fortune Bay with the Labrador Current during the winter period. A persistent wind event from the south could transport larvae in the surface layers at a much faster rate than would the inshore branch of the Labrador Current. However, the prevailing wind direction at St. Lawrence on the southern part of the Burin Peninsula for January and February 1981 was from the west with wind from the south only 1% of the time in January and 6% in February 1981 (Anonymous 1981). A peak wind event from the SSE on February 9 did not persist into the next day when winds were again from the west. We conclude, therefore, that it is unlikely that the yolk-sac larvae found within Fortune Bay in February 1981 were transported from St. Pierre Bank. More likely, these larvae were spawned in Fortune Bay. Such spawning is consistent with evidence from hydrographic charts that indicate many areas of gravel and sand mixtures in Fortune Bay. According to Reay (1970), this is the preferred spawning substrate for sand launce.

Yolk-Sac Absorption

Sixty-two percent of the larvae collected in February 1981 contained yolk sacs. The mean length of those in which the absorption of yolk-sac (+ oil globule) was complete was 8.1 mm while those with absorption incomplete had a mean length of 7.4 mm. This is consistent with published records. Smigielski et al. (1984) gave yolk-sac absorption lengths of 7.2-7.41 for laboratory reared *A. americanus*, and Richards (1965) found that oil globule absorption was complete between 5 and 7.5 mm.

DISCUSSION AND CONCLUSIONS

The conclusion from the data collected during the day-night investigations is that smaller yolk-sac larvae in February and larger larvae in June are more abundant or more available to the gear at night. It is difficult to discern a particular pattern of diurnal and vertical migratory behavior for sand lance larvae from the literature because documentation on the subject has not been consistent. The observation that larger larvae in June are more abundant at night is not unusual and may be attributable to net avoidance (Norcross et al. 1961; Richards and Kendall 1973; Potter and Lough 1986). The observation that yolk-sac lar-

vae are more abundant in surface night sets appears unusual since Richards and Kendall (1973) found that in winter larvae 8-17 mm were more abundant in deep tows at night and surface tows during the day. Avoidance behavior does not appear to develop until a size of greater than 10 mm (Norcross et al. 1961; Potter and Lough in press). Assuming the same for larvae in Fortune Bay, it is not likely that yolk-sac larvae were avoiding the gear during the day. Although it is not possible to make a definite conclusion on vertical migration with the relatively small number of larvae, the data suggest that yolk-sac larvae in February are also capable of vertical migration.

Our analyses of sand lance larvae from Fortune Bay have demonstrated for the first time the occurrence and probable spawning of the slender-bodied *A. dubius* in coastal waters in Newfoundland. Previous studies by Winters (1970) have indicated the occurrence of only the deep-bodied form *A. americanus* in Newfoundland bays with *A. dubius* being found exclusively on the offshore banks. This finding is significant in light of the current confusion as to the appropriate taxonomy of the sand lance populations in the Northwest Atlantic. Both *A. americanus* and *A. dubius appear to* resemble *A. marinus* which is currently considered to occur only in European waters (Reay 1970), and the characteristics used to separate the two Northwest Atlantic types from each other and from *A. marinus* are sometimes tenuous particularly in southern parts of the range. In the Newfoundland area, however, *A. americanus* and *A. dubius* maintain distinct meristic counts. The occurrence and probable spawning of *A. dubius* in a coastal area, formerly considered to be inhabited exclusively by *A. americanus* (Winters 1970), indicates sympatry. This provides evidence that the two forms are reproductively isolated and therefore separate species. This is substantiated by the fact that the meristics described for *A. dubius* larvae in Fortune Bay and those offshore (Winters 1970) are identical.

We have also demonstrated that the spawning season of sand lance in Fortune Bay, Newfoundland, is protracted and probably extends from December to May or June. This spawning period is much longer than in southern areas of the Northwest Atlantic where the spawning season in inshore waters is from the period December to February (Richards 1982). It is possible that this extended spawning season is also a result of the mixture of the two species in Fortune Bay; however, the polymodality in the length frequency of large *A. dubius* (>20 mm) larvae in Fortune Bay suggests that an extended spawning season may be characteristic of this species in coastal Newfoundland waters.

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NOTES

HEART AND GILL VENTILATORY ACTIVITY IN THE LOBSTER, *HOMARUS AMERICANUS*, AT VARIOUS TEMPERATURES

Heart rate and gill ventilatory activity have been suggested as useful measures of the physiological condition of decapod crustaceans and their response to various environmental conditions. Several authors have described altered ventilatory and heart rates in response to such variables as temperature, salinity, and dissolved oxygen (Uglow 1973; Cumberlidge and Uglow 1977; Taylor 1977; Hagerman and Uglow 1979). Price and Uglow (1980) also discussed the applicability of these measures in studies of pollutant stress where they described the effects of copper, cadmium, and zinc on the heart and ventilatory rates of *Crangon crangon*. The mechanics of ventilatory reversals of decapod crustaceans have also been described; for example, the reverse ventilatory pulses (coughs) produced by the American lobster, *Homarus americanus*, during a muscular compression of the branchial chamber probably provide irrigation to the posterior area of the gills or help to clear detritus from gill surfaces (Wilkins and McMahon 1972; Bill and Thurberg 1985). The frequency of the lobster cough response increases after exposure to a variety of waterborne chemicals, and it has been suggested that this response might be a useful measure for detecting aquatic pollutants (Bill and Thurberg 1983, 1985). Before these heart and ventilatory measures can be employed as monitoring tools, however, baseline information should be collected on their seasonal variability under normal, unpolluted conditions, against which to interpret any stress-induced change. This study addresses the relationship between heart, gill-bailer, cough rate, and seasonal water temperature.

Methods

Adult American lobsters (61.4-91.2 cm carapace length) were trawl-collected in Long Island Sound off Milford, CT, and held in running seawater at ambient temperature. Seawater for this building is taken from Milford Harbor, a harbor with good tidal flushing and no industrial development. The pollutant content here is very low; for example, seawater cadmium is <0.5 ppb, mercury <1 ppb, lead <5 ppb, and copper 2-4 ppb. The PCB levels (0.67 ppm, wet weight) in blue mussels, *Mytilus edulis*, from Milford Harbor are typical of levels found in molluscs along the U.S. east coast (Farrington et al. 1983; Greig and Sennefelder 1985). Although no area of Long Island Sound can be considered "pristine", this area has excellent water quality for holding and rearing marine animals as evidenced by a 50-yr laboratory history of marine invertebrate culture. The salinity range is 26-28 ppt with occasional brief low salinity episodes during extreme rains (not during this study, however) and the dissolved oxygen levels remain at or near saturation at the temperatures in this study. The lobsters were fed chopped clams, fish, or crabs daily. Heart, gill-bailer, and cough rates were monitored with 6 mm silver disc electrodes, an impedance converter, and an amplified polygraph recorder, following the methods described in Bill and Thurberg (1985). Measurements were made at 2°, 6°, 10°, 14°, and 18°C over a 1-yr period. Each lobster was allowed to acclimate to temperature for at least 2 weeks before testing. Between 9 and 23 lobsters were monitored at each temperature for a 1-h period. Rates were calculated on a per-minute basis.

Results and Discussion

Crustacean metabolism varies with temperature (Wolvekamp and Waterman 1960; Taylor et al. 1977, 1973). Aiken (1980) observed that elevated temperatures accelerate the metabolic processes in lobsters, although the parameters were not defined. The data presented here confirm this increase in metabolism using three physiological parameters. Figure 1 shows the increasing frequency of heart and gill-bailer rates as the temperature rose from 2° to 18°C. Cough rate also increased with increasing temperatures (Fig. 2). Bill and Thurberg (1983) reported a cough rate of 0.4 coughs/minute at 10°C in this species, a rate similar to that reported in this study at 10°C (0.32 coughs/minute). The data reported here present a full seasonal profile of three important metabolic measures. They provide a

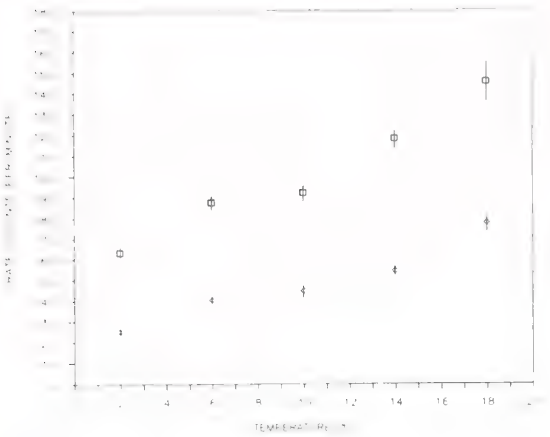

FIGURE 1.—Temperature (°C) versus heart (◇ and gill bailer (□) rate (counts per minute) of the American lobster, *Homarus americanus*, at 2°, 6°, 10°, 14°, and 18°C. Each point is the mean value of 9-23 lobsters and the vertical line is ±1 standard error.

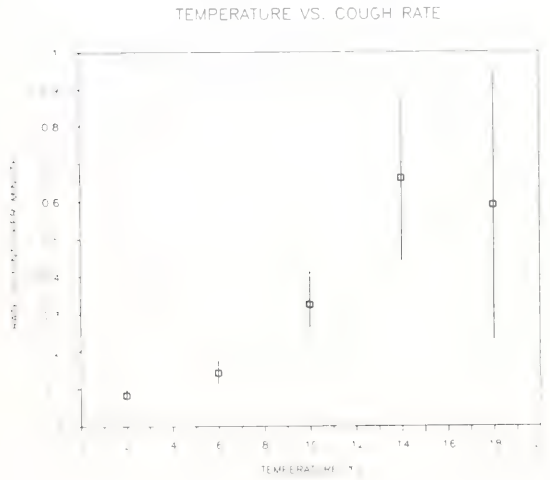

FIGURE 2.—Temperature (°C) versus cough (□) rate (counts per minute) of the American lobster, *Homarus americanus*, at 2°, 6°, 10°, 14°, and 18°C. Each point is the mean value of 9-23 lobsters and the vertical line is ±1 standard error.

comprehensive and easy-to-interpret baseline against which to compare similar measures made on lobsters from areas suspected of pollutant impact.

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A METHOD OF SIMULTANEOUSLY TAGGING LARGE OCEANIC FISH AND INJECTING THEM WITH TETRACYCLINE

A simple method of marking large oceanic fish such as yellowfin tuna, *Thunnus albacares*, and wahoo, *Acanthocybium solandri*, for age determination studies is described. The method, developed for tagging and injection with tetracycline of yellowfin tuna >45 kg from the deck of sport fishing vessels, is easily adaptable to other species, including billfish and possibly marine mammals.

The use of calcium-specific markers, such as oxytetracycline (OTC), to validate the temporal significance of natural marks in hard parts has become increasingly widespread. Validation is recognized as a basic requirement of age and growth studies (Beamish and McFarlane 1983). OTC is usually administered orally, intraperitoneally, or intramuscularly (Weber and Ridgway 1967; Wild and Foreman 1980; Campana and Neilson 1982). Boating and restraining while OTC is injected causes stress and trauma to the fish and may result in injury to the tagger when large, powerful pelagic fish are tagged. Nevertheless, biologists from the Inter-American Tropical Tuna Commission (IATTC) have successfully tagged and injected medium-sized (up to 36 kg) yellowfin tuna (Anonymous 1982) where, using multiple poles (two pole method, described in Godsil 1938), the crew pulled the fish onto the padded aft deck (Bayliff and Holland 1986) of a dedicated tuna baitboat. Although this method would probably suffice when tagging even larger fish, dedicated vessels are costly and there is no guarantee of locating adequate-sized fish during the charter period. Opportunistic tagging by the crews of long-range sportfishing boats, which frequently capture large tuna but lack gear to handle live fish on deck, was an attractive prospect.

Methods and Materials

A device used for administering drugs to zoo animals (Extend-O-Jector[1], model A, Kay Research Products, Hyde Park Bank Bldg., Suite 503, 1525 East 53rd St., Chicago, IL 60605 USA) was modified (Fig. 1) by adding a stainless steel dart tag applicator held at an appropriate distance with 13 mm thick PVC sheet press-fitted to the distal end of the injector head. The applicator was then fastened to the grooved base of the injector head with a hose clamp, stabilizing it during use. Other types of applicators, such as those used for metal anchor tags (Bayliff and Holland 1986) can be easily substituted. Depending on the tag type, a rubber band may be used to hold the tag in place during application.

The device utilizes either a 3 to 5 cc disposable syringe and a 2-in (51 mm) needle. For tunas, a 17 gauge needle provided the best combination of sufficiently high delivery rate and minimum puncture diameter.

As the decks of most long-range sportfishing boats are quite far off the water (2 m), the device was bolted inside a 25 mm ID telescoping tubular aluminum pole, the type normally used with swimming pool cleaning equipment. The length may then be adjusted to suit individual situations.

When a large tuna was captured by an angler, the tag and injection was administered below the second dorsal fin while the fish was still in the water. Through trial and error, application was found most efficient when the device is continuously pushed toward the fish's body after initial insertion of the applicator needles. Best results are obtained when the device is kept as near to perpendicular to the body of the fish as possible, preventing the needles from bending, damaging the fish, or both. The fish is released by removing the hook by jerking the bend of the hook with a gaff forwards while pulling the line backwards, or cutting the leader as close to the hook as possible. Under certain conditions, free-swimming fish found at the surface may be tagged and injected.

A previous experiment (unpubl. data, Inter-American Tropical Tuna Commission, La Jolla, CA) determined that doses as low as 10 mg/kg body weight formed readable marks in the vertebrae of mackerel, *Scomber japonicus*. Wild and Foreman (1980) and Foreman (1987) determined that a dosage of 27 mg OTC/kg body weight formed a brilliant mark in the otoliths of yellowfin and skipjack, *Katsuwonus pelamis*, tunas and in otoliths and vertebrae of bluefin tuna, *Thunnus thynnus*. For large fish (near 45 kg), the volume required using standard veterinary injectable (100 mg/mL) OTC would be unmanageable; a more concentrated form (200 mg/mL; Pfizer Liquamycin LA-200) was substituted. Because the marks formed in smaller fish were sufficiently bright, the dose was reduced by half, to about 13.5 mg/kg.

[1]Reference to trade names does not imply endorsement by the National Marine Fishers Service, NOAA.

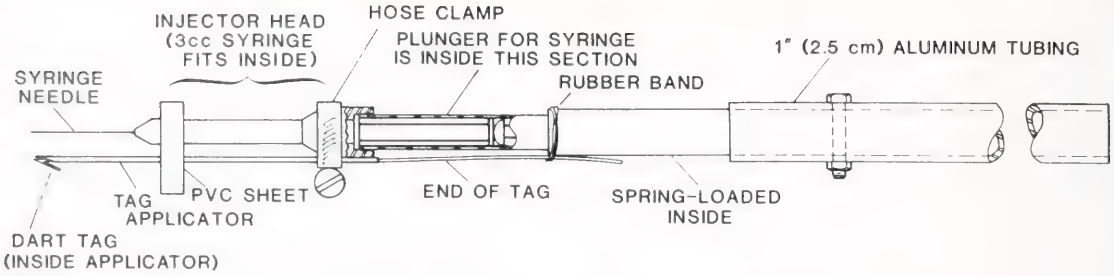

FIGURE 1.—A tag and injection device for large pelagic fish.

Results and Discussion

On the night of 27-28 January 1986, the crew and passengers of a 34 m long-range sportfishing boat, *Royal Polaris*, tagged, injected, and released 36 yellowfin tuna, all estimated to be >45 kg. Six of these fish were recaptured from 14 to 83 days later, indicating that the tagged fish were active and feeding.

Differences in return rates between this method and the padded deck method (Table 1) are possibly due to such factors as differences in size and age of the fish tagged, fishing effort in the tagging area, or the amount of stress caused by different fishing methods, rather than some characteristic of the pole method.

The otoliths from recaptured fish displayed the yellow-green fluorescent mark when viewed under ultraviolet light, but the marks appeared much fainter than those on otoliths returned from the program which used a padded deck. Since the dosage each fish received was monitored by the amount (if any) left in the syringe after application, failure of the device to deliver the full amount of OTC was ruled out. Similarly, the needle size was nearly the same for both treatments, and pore seepage is assumed equal. There were, however, differences in the type of OTC used. Liquamycin LA-200, used with the pole device, was found to contain a slow-release agent (2-pyrrolidone) which extends the antibiotic effect over time. Evidently the agent also slows deposition of the fluorophors such that their concentration in the area of osteogenesis and hence the brilliance of the mark is diminished. I recommend that an OTC solution without slow-release agents be used, e.g., Anchor Oxy-Tet 100, as in previous experiments.

TABLE 1.—Comparison of tag return rates from the padded deck method (unpubl. data, Inter-American Tropical Tuna Commission, La Jolla, CA) and pole injection device method for yellowfin >100 cm (20.5 kg) at release.

	Releases	Returns	Percent
Padded deck	49	16	32.7
Pole device	36	6	16.7

Acknowledgments

I appreciate the assistance of J. Allen and his staff at the San Diego Wild Animal Park, and T. Dunn for input into the design of the injection equipment, and the crew and passengers of the *Royal Polaris*, especially J. Heyn, W. Lang, F. LoPreste, and C. Miller, for their assistance and dedication to the project.

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SECOND RECORD OF THE KAWAKAWA, *EUTHYNNUS AFFINIS*, FROM THE EASTERN PACIFIC OCEAN

Although the kawakawa, *Euthynnus affinis* (Cantor 1849), is widely distributed throughout the warm waters of the Indo-West Pacific (Yoshida 1979), it is replaced by the black skipjack, *E. lineatus* Kishinouye, in the eastern Pacific. There is only one previous record of *E. affinis* in the eastern Pacific. That specimen, 361 mm fork length (FL), was reported from Los Angeles Harbor, CA, in 1952 (Fitch 1953). The second documented occurrence of *E. affinis* from the waters of the eastern Pacific is recorded in this note.

The specimen, *E. affinis*, 920 mm FL and 13.15 kg, was caught by Ronald Nakamura using hook and line from the long-range San Diego-based sport-fishing boat, *Royal Polaris*, on 17 December 1986, off Clarion Island (lat. 18°22′N, long. 114°44′W) in the Revillagigedo group. The specimen has been deposited in the Scripps Institution of Oceanography fish collection (SIO 87-70).

The morphometric and meristic characters for the specimen are given in Table. 1. The measurements were taken according to the methods of Godsil and Byers (1944) and Gibbs and Collette (1967). The external characters of this specimen agree with Godsil's (1954a) description of the species. The wavy oblique markings on each side of the dorsal surface, no dip in the lateral line below the second dorsal fin, and the several black to gray spots scattered over a relatively wide area between the pectoral and pelvic fins are characteristic of most specimens of this species. Furthermore, the morphometrics for this specimen are within the ranges for those body proportions reported by Godsil (1954b) and are closer to the morphometrics for *E. affinis* from Hawaii, rather than from Japan.

The internal characters also appear to agree with Godsil's (1954a) description of the species. High-quality radiographs produced by computer-assisted tomography (C.A.T.) scanning equipment were utilized for examing skeletal characters. The vertebral count is 20 + 19 = 39, and the radiographs showed no bony protuberances on any of the caudal vertebrae. However, no vomerine teeth were present. Although there was no indication of their previous presence, their absence could be explained by wear in this presumably old specimen. Nevertheless, the primary characters distinctive of *E. affinis*, 39 vertebrae, the total gill raker count of 31, and the absence of bony protuberances on the caudal vertebrae, leave no doubt on the identity of this specimen.

The occurrence of *E. affinis*, as well as the first documented occurrence of this specimen in the eastern Pacific, should be considered extremely rare events. No specimens of *E. affinis* were noted, during 1980-82 while personally examining a few thousand specimens of *E. lineatus* landed by commercial tuna vessels operating in the eastern Pacific. One of the remarkable fea-

TABLE 1.—Summary of morphometric and meristic data. The measurements are in millimeters.

Character	Measurements (mm)
Fork length	920
Head length	263
Snout-first dorsal	301
Snout-second dorsal	552
Snout-anal	590
Snout-ventral	291
Max. body depth	232
Max. body width	156
First dorsal-ventral	225
First dorsal-anal	385
Ventral-vent	310
Base first dorsal	238
Base second dorsal	72
Base anal	61
Pectoral length	138
Anal length	65
Diameter of iris	29
Maxilla length	97
Snout-posterior of eye	106
	Counts
Dorsal spines	15
Second dorsal rays	13
Dorsal finlets	8
Anal rays	14
Anal finlets	7
Pectoral rays	26
Gill rakers	8 + 1 + 22 = 31

tures of *E. affinis* is its extremely large size, particularly its weight of 13.15 kg, as this specimen represents the heaviest *E. affinis* documented. The previous documented record of maximum size for *E. affinis* was 11.79 kg based upon a specimen captured in Merimbula, NSW, Australia in 1980 (Anonymous 1986).

It is interesting that the maximum size records established for the black skipjack, *E. lineatus*, and the yellowfin tuna, *Thunnus albacares*, are based upon sport-caught specimens from the Revillagigedo group of islands. The fact that many species tend to be longer lived and reach maximum sizes in the northern latitudinal ranges of their distributions, apparently pertains to the aforementioned species of tunas, as well. In the case of this record specimen of *E. affinis*, although found outside its normal geographical distribution, the maximum size was attained in this same region of the Pacific Ocean.

Acknowledgments

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CONTRIBUTION TO THE LIFE HISTORY AND REPRODUCTIVE BIOLOGY OF GAG, *MYCTEROPERCA MICROLEPIS* (SERRANIDAE), IN THE SOUTH ATLANTIC BIGHT[1]

The gag, *Myceteroperca microlepis*, is a demersal serranid found along the southeastern coast of the United States and in the Gulf of Mexico (Smith 1971; Fischer 1978). Throughout its range the gag is of both commercial and recreational importance. Because of its relatively slow growth rate (Manooch and Haimovici 1978) and desirability, overfishing is of wide concern.

The gag is a protogynous hermaphrodite, and McErlean and Smith (1964) suggested that sexual transformation occurs during the 10th or 11th year. Spawning occurs from January to March off the west coast of Florida (McErlean 1963), and the maximum reported age is 13 years in both the Gulf of Mexico (McErlean 1963) and the South Atlantic Bight (SAB) (Manooch and Haimovici 1978). Microscopic examination of the gonads is necessary for definite sexual identification, but gonad morphology has not been specifically described. The purpose of this study is to provide new information on the age, growth, and reproductive biology of this important species, including a description of the morphology of gag ovaries and testes.

Methods

Most samples were obtained from the commercial hook and line fishery, and others were collected on research cruises aboard the RV *Dolphin*, RV *Oregon*, and RV *Lady Lisa* from 1976 to 1982. Specimens were measured (total and standard lengths), weighed, and sagittae removed from the otic capsule through the branchial chamber. Otoliths were stored dry and later viewed in a dish of cedar wood oil with reflected light over a dark background using a binocular microscope. Since opaque bands in larger otoliths were thin and often too crowded near the edge to permit accurate counting, cross sections (approximately 0.5 mm thick) were made on the dorsoventral plane of the otoliths through the center with a diamond dicing wheel mounted on an ISOMET[2] low speed saw. Sectioned otoliths were viewed in

[1]Contribution No. 226 of the South Carolina Marine Resources Center, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

the same manner as whole otoliths. If two readings by a single observer did not agree, otoliths were deleted from analyses. Additional verification of counts was then obtained from a second observer who read 200 otoliths (35%) selected randomly.

Because monthly samples did not contain similar porportions of large and small fish, calculations of monthly mean marginal increments of sagittae were biased. For instance, if primarily small fish are sampled in one month followed by mostly large fish in the next month, the mean marginal increment will decrease regardless of the time of year. To alleviate this bias, marginal increments were standardized by converting each measurement to a proportion of the maximum recorded for that age group. Thus, a measurement of 2.5 ocular units in an age group for which the maximum is 10.0 becomes equivalent to a measurement of 0.5 ocular units in an older group for which the maximum is 2.0.

Sex and reproductive conditions were determined from histological sections of gonads, which were preserved in 10% formalin, and later processed through an Autotechnicon Duo Model 2A automatic tissue processor, then embedded in paraffin, and sectioned with a rotary microtome at approximately 7 μm (Humason 1972). Tissues were then stained with Harris' hematoxylin and counterstained with eosin-Y. Sexes were identified as male, female, and hermaphroditic female or "transitional" (gonad primarily ovarian, with some traces of active testicular tissue present). Maturity was described following the synopses listed in Waltz et al. (1982). Terminology used in histological descriptions follow Hyder (1969), Combs (1969), and Wallace and Selman (1981).

Results

A total of 1,039 gag ranging in total length (TL) from 153 to 1,150 mm was examined for life history information. Of the 652 otoliths on which age determinations were attempted, 87% showed discernible rings verified by two readings. No otoliths were deleted from analyses because of disagreement between primary and secondary readers. Marginal increment measurements from the outer edge of the last opaque band to the dorsal margin of whole sagittae indicate that these bands are laid down in late spring to midsummer. Bands are apparently laid down earlier and over a longer time period (May-August) in ages ≤VIII than in older gag. Although sample sizes of fish ≥age IX on which marginal increments were measured are small in relation to those of younger gag, it appears that ring formation is concentrated in August (Fig. 1). Twenty-two age groups were identified (Table 1).

The gag ovary is a hollow, bilobed organ suspended in the posterior region of the body cavity from the swimbladder by mesenteries. Blood vessels and nerves enter the gonad at the anterior point of each lobe's suspension and course medially to the mesenteries along the dorsomedial surface of each lob. The lobes fuse posteriorly, their

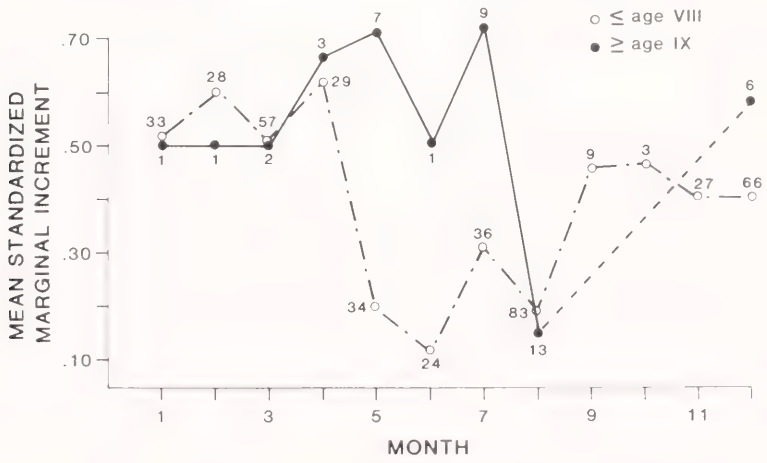

FIGURE 1.—Mean standardized marginal increments by month for gag ≤age VIII and ≥age IX, and sizes of monthly samples.

TABLE 1.—Observed mean lengths (mm), weights (kg), and sample size by age for *Mycteroperca microlepis*.

Age	Number	Total length (mm)	Standard length (mm)	Weight (kg)
0	14	187	153	0.087
1	17	347	293	0.605
2	18	466	383	1.263
3	26	575	470	2.104
4	49	677	555	3.881
5	80	767	641	5.558
6	102	824	686	6.040
7	91	865	729	7.612
8	51	895	751	8.454
9	21	936	789	9.810
10	19	959	807	10.491
11	23	993	826	11.399
12	7	1,004	841	13.327
13	4	1,048	884	14.950
14	2	1,066	905	13.000
15	2	1,096	927	14.748
16	9	1,064	905	14.495
17	10	1,076	904	14.767
18	10	1,068	887	14.310
19	5	1,087	924	14.074
20	5	1,071	896	15.150
21	1	1,125	950	15.400
22	1	1,124	946	—

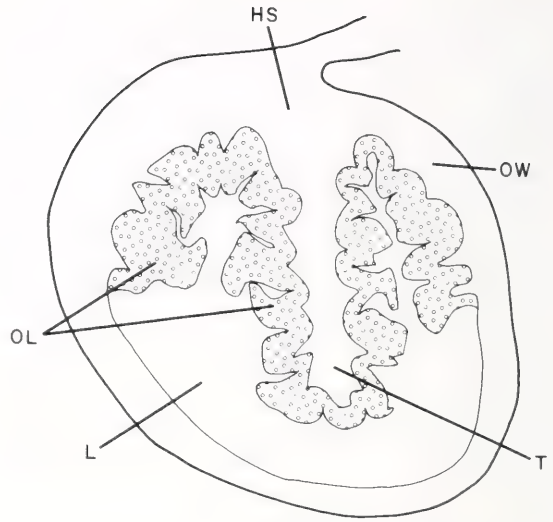

FIGURE 2.—Schematic representation of a cross-sectioned gag ovary (diameter = 3 cm). HS = halar stroma, L = lumen, OL = ovarian lamellae, OW = ovarian wall, T = "Typhlosole-type" invagination of the dorsal wall.

lumena forming a common oviduct. The lumena are incompletely lined with folded germinal epithelium (ovarian lamellae) within which oocytes develop and mature. The ventral regions of the lumena remain void of lamellae, and these alamellar areas are contiguous with the alamellar oviduct. In addition to the dorsal and lateral walls of the lumena showing lamellar development, there is a "typhlosole-type" continuation of the dorsal gonad wall projecting into each lumen. This projection of connective tissues into the center of the lumen apparently allows additional surface area for attachment of ovarian lamellae (Fig. 2).

During the sexual transition phase, testicular growth fills the existing ovarian lamellae, displacing and possibly dislodging the already degenerating oocytes. Transitional gonads were rarely found, and there were no cases of simultaneous development of gonad tissues. Male gonads retain the somatic morphology of the ovary. Testicular tissue is arranged in "false lamellae", primarily suspended from the "typhlosole-type" structure. Sperm sinuses form peripherally in what was previously the ovarian wall and continue posteriorly becoming the vas deferens within the oviduct wall. The vestigial ovarian lumena and oviduct remained in all testes examined. All testes also possessed many residual oocytes, some as large as 500 μm in diameter.

Females made up 84% of the gag which were sexed. Examining the percentage in each age class, we found that 28% of age III, 51% of age IV, and all older female gag had mature ovaries. Immature gag ranged from 290 to 680 mm TL, whereas the smallest mature female was 600 mm TL. Male gag accounted for 15% of the animals sexed and were found in ages V through XX (no sex available for age XXI and XXII fish). No males were found smaller than 790 mm TL (Fig. 3) and no juvenile males were found. Gag with transitional gonads made up 1.25% of all the groupers sexed and occurred in ages V through XI. The size range for fish undergoing sex succession was from 750 to 950 mm TL (Fig. 3).

The gag spawns once a year in late winter-early spring. Analysis of the relative abundance of developing, ripe, and postspawned gonads indicated that peak spawning activity was reached in late March and early April (Fig. 4) in the SAB.

Discussion

Use of whole sagittae in aging gag has been validated (McErlean 1963), and Matheson et al. (1986) successfully validated the use of sectioned sagittae to age the congeneric scamp, *Mycteroperca phenax*. These studies together with the present data provide good evidence that sagittal

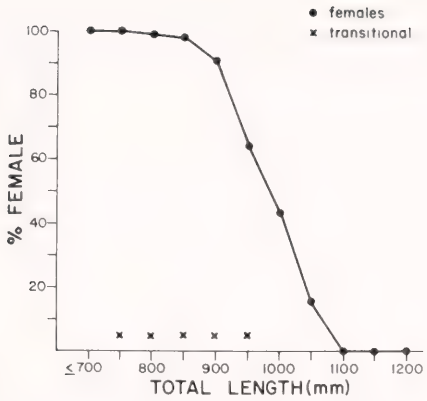

FIGURE 3.—Percent female gag by length class, and occurrence of transitional gag.

rings detected in the present study are annual in nature. While the importance of adequate validation has been well documented (Beamish and McFarlane 1983), it has become increasingly clear that annulus formation in many species can take place over an extended period, making it difficult to pinpoint this event in time. Peak annulus formation covered a 3-mo period for the groupers *Epinephelus drummondhayi* (speckled hind) and *E. niveatus* (snowy grouper) (Matheson and Huntsman 1984). Thus, the May-August period of peak ring formation for younger gag in the present study is not unusually long. Reasons for differences between ages ≤VIII and ≥IX in timing of peak annulus formation are not apparent. However, that the differences are at least partially based on sex is probable since the younger fish are predominately female while approximately 60% of the older group are male. A comparison strictly between sexes was not possible since samples of males available for measurement were obtained in only 5 months.

The use of sectioned sagittae greatly enhanced clarity among the higher age groups and allowed for greater distinction between rings in comparison to whole otoliths. Beamish (1979) found that sectioned otoliths of the Pacific hake, *Merluccius productus*, gave a more accurate account of age, especially when thick otoliths with poorly defined annuli were encountered. This appears to be true for the gag, as well. Twenty-two age groups were distinguished in the present study, similar to the 21 age groups reported for the scamp (Matheson et al. 1986), compared with previous reports of 13 age groups for the gag (McErlean 1963; Manooch and Haimovici 1978). The nine groups not detected previously do not represent just an increase in the percentage of readable otoliths (present study: 87%; McErlean 1963: 87%; Manooch and Haimovici 1978: 79%). Rather, it appears that additional annuli are present in the otoliths of the larger size classes that were not detected in previous studies using whole otoliths. For instance, the oldest fish collected by Manooch and Haimovici (1978) was age XIII and 1,201 mm TL, longer than any gag aged in the present study and 77 mm longer than the age XXII fish (Table 1).

Moe (1969) described the reproductive biology of the red grouper, *Epinephelus morio*, and many aspects of the development and sex succession schedules are similar to those found in the gag.

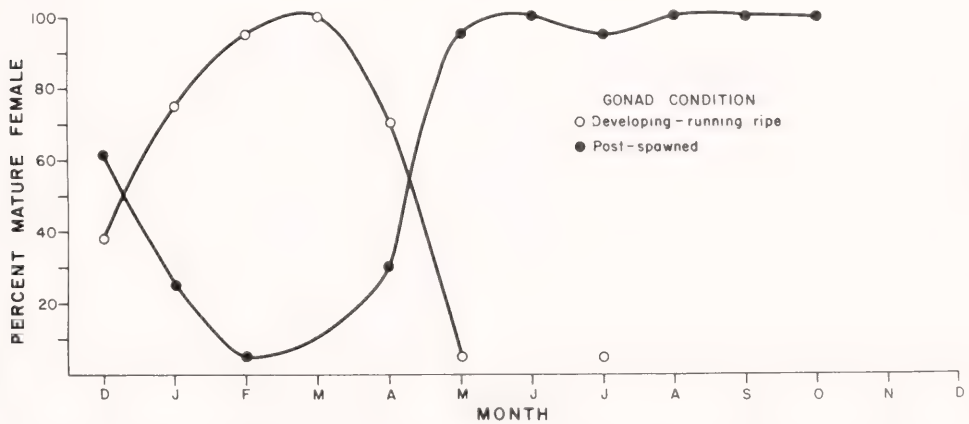

FIGURE 4.—Maturity stages of female gag by month of capture, illustrating the late winter-early spring spawning season.

The actual morphology of the gonad, however, differs from that described for red grouper. Moe (1969) cited Smith's (1965) description of an *E. fulvus* ovary, but Smith did not mention the "typhlosole-type" structure from which ovarian lamellae are suspended that was found in gag gonads in the present study. This structure is also found in *M. phenax*, *M. interstitialis*, *E. adscencionis*, *E. drummondhayi*, *E. flavolimbatus*, and *E. niveatus* (Roumillat, unpubl. data) and may be present in other groupers.

Although Moe (1969) found only 1.43% of red groupers undergoing sexual succession, the percentage of fish with transitional gonads was even lower in the gag (1.25%). These frequencies are much lower than the transitional frequencies of such sympatric species as *Centropristis striata* (14%; Wenner et al. 1986), *Calamus leucosteus* (10-13%; Waltz et al. 1982), *Pagrus pagrus* (10%; Roumillat, unpubl. data), and *Hemanthias vivanus* (9%; Hastings 1981). A rapid rate of sex succession is probably the reason for the low frequency of transitional gonads found. Smith (1965) and Moe (1969) suggested that other groupers have a very quick rate of succession, and Fishelson (1970) and Shapiro (1981) have shown that *Anthias squamipinnis* can change sex within a few weeks.

Despite suggestions that gag transform to males during their 10th or 11th year (McErlean and Smith 1964), it is evident that sexual succession occurs at younger ages. Only seven transitional gag were collected, and of the five that were aged, there was one each in age groups V, VI, VII, VIII, and XI. However, age X was the group in which the sex ratio approximated unity. The age of first maturity for females was lower than the previously speculated fifth or sixth year (McErlean and Smith 1964), and 28% of age III, 51% of age IV, and all older femal gag had mature gonads. Thus, there may be significantly more gag (all females because of protogyny) producing gametes than indicated in the literature, suggesting a greater ability to rebound from intensive overfishing than previously suspected.

Acknowledgments

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AGE AND GROWTH, REPRODUCTIVE CYCLE, AND HISTOCHEMICAL TESTS FOR HEAVY METALS IN HARD CLAMS, *MERCENARIA MERCENARIA*, FROM RARITAN BAY, 1974-75.

Raritan Bay has historically supported an abundant hard clam, *Mercenaria mercenaria* L., resource. It was considered the most important commercial species in the bay with an estimated total value of 34 million dollars in 1963 (Jacobsen and Gharrett 1967). Campbell (1967) reported a total standing crop of 4.8 million bushels of clams for the Bay for the same year (3.4 million bushels in New York waters and 1.4 million bushels off New Jersey). More recent estimates are unavailable.

Raritan Bay waters have historically received various domestic and industrial wastes, some of which have had adverse effects on its shellfish resources and fisheries. Raritan Bay was closed to harvesting of hard clams on 1 May 1961, after an epidemic of human infectious hepatitis was traced to the consumption of raw clams from the bay (Campbell 1967). The closure remains in effect to the present time. Zoellner (1977) reviewed the nationwide water quality problems related to shellfish and included Raritan Bay as one of the case studies in the report.

Bivalves accumulate various biological and chemical contaminants by mechanisms related to their filter-feeding habits and transport across their mucous-covered, semipermeable soft body tissues (Goldberg 1957; George 1982). The accumulation of heavy metals, pesticides, polychlorinated biphenyls (PCB's), oil and dispersants, disease causing bacteria, viruses, fungi, parasites, and toxic phytoplankton have serious public health implications and may also adversely affect bivalve resources. Zoellner (1977) has reviewed natural and manmade conditions affecting bivalve populations, including specific studies of the effects of heavy metals, pesticides, and PCB's. McCormick et al. (1984) reviewed physical and sediment characteristics of Raritan Bay, studies of benthic organisms, plankton, and fish, and impact of pollution from sewage, organic chemicals, and heavy metals.

The present study was undertaken to assess potential impacts of contaminants in Raritan Bay on the spawning potential of hard clams. Monthly samples were collected from three study areas within the bay to obtain measurements of the shells, soft body tissues for observations of general condition, and gonadal tissues for observations of the reproductive cycle. Selected specimens were chosen to determine age and growth, and special tissue samples were collected for histochemical tests of certain metals. Published hydrographic conditions and assessment of pollutants in Raritan Bay are discussed in relation to sample results.

Methods

Campbell (1967) described the distribution of hard clams in Raritan Bay and, based on his findings, sites were chosen for repeated collections. The sites were Ward Point, New Dorp Beach, and Horseshoe Cove (Fig. 1). Each was sampled at about monthly intervals beginning on 21 February 1974 and ending on 7 April 1975. The clams were collected by towing a drag-type, nonhydraulic dredge with a 12-in (30 cm) wide knife from the U.S. National Marine Fisheries Service (NMFS) RV *Rorqual*. Tows were made at each site until 30 or more clams larger than 50 mm in shell length were caught. Special collections were made at Ward Point and New Dorp Beach on 1 November 1978 to obtain tissues for histochem-

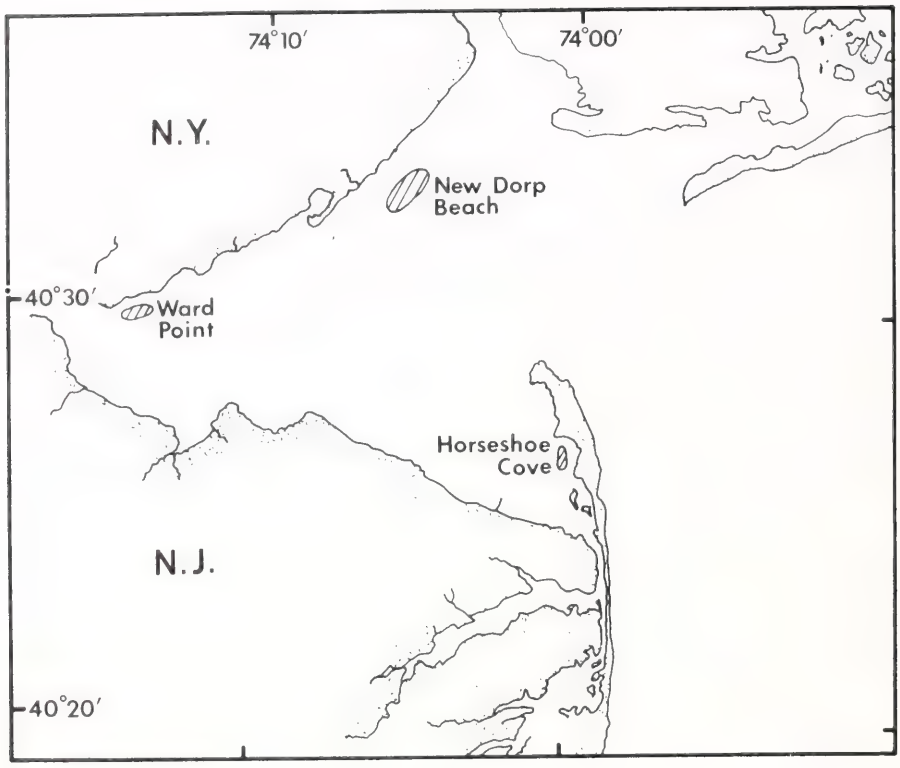

FIGURE 1.—Locations sampled for hard clams, *Mercenaria mercenaria*, in Raritan Bay during 1974 to early 1975 and 1978.

ical tests of some metals, using the same dredge operated from the NMFS RV *Kyma*.

Following sampling operations at each site, the length (longest anterio-posterior dimension), height (deepest dorsoventral dimension from the umbo to ventral shell margin) and width (thickest lateral dimension) of each clam shell was measured to the nearest millimeter with vernier calipers. About 20 clams were then opened and the meat and shell liquor packaged for immediate freezing. Later measurements were made of the drained meat weight, dry meat weight, and percent solids by methods outlined by Ropes (1971a) for other bivalves.

Specimen shells for age and growth observations of hard clams were chosen from Ward Point and New Dorp Beach samples, since clams from these sites exhibited extremes in shell and weight measurements. The selection included five clams in a sample having the smallest mean size, five in a sample having the largest mean size, and those in a sample having a mean size nearly equal to the grand mean for all samples taken at the particular site. The shells were radially sectioned and the cut edge polished to a high luster, as described by Peterson et al. (1983) to facilitate detection of annual growth lines.

Ten additional clams were opened and the soft body tissues were removed for preservation in Bouin's fixative. Methods used for dehydrating, embedding, sectioning, and staining gonadal tissues to prepare slides for microscopic examination of the reproductive cycle were as outlined by Ropes and Stickney (1965) and Ropes (1968). Stages in the development of gonadal tissues were established. The progressive development of sex cells through early to ripe condition and eventual expulsion by spawning activity was a basis for evaluating reproductive viability. Failure to complete all stages of a cycle was considered an indication that the clams were being impacted by environmental conditions.

Specimens were collected for histochemical tests on 1 November 1978 (10 hard clams and 2 oysters from Ward Point and 10 hard clams from New Dorp Beach). The soft body mass of each

specimen was removed on the vessel within an hour of capture. One cm-thick slices were dissected from the central body mass of each specimen and immersed in a vial of fixative appropriate for the histochemical test. Samples were then transported to the NMFS laboratory at Oxford, MD, where slides were prepared for microscopic examination. The following histochemical tests were performed:

1. Inorganic iron. Perl's (1867) reaction, reported in Casselman (1959), to produce ferric ferrocyanide from ferric ions (Fe^{+++}).
2. Arsenites and arsenates. The method of Castel (1936), reported in Pearse (1972), to precipitate the cupric salts of arsenites and arsenates (As^{+++}, As^{++++}).
3. Lead. The method of Cretin (1929), called the chromate method from a reaction with neutral potasssium dichromate, was used, together with the rhodisonate method (Pearse 1972). Both methods are reported in the latter paper.
4. Copper. A method is reported by Uzman (1956) to localize copper by direct treatment of the tissues with rubianic acid. After examining the results of this treatment, the intensification technique to release copper "bound" proteins suggested by Uzman (1956) was also tried.

Results

Hard clams were generally more easily collected at the New Dorp Beach and Horseshoe Cove sites than at Ward Point. Bottom substrata in the dredge with the clams was predominantly a black silty-sand at New Dorp Beach and a relatively clean sand with some shell at Horseshore Cove, but at Ward Point, shell (mostly from oysters) was a major component of the black mud substrata. Live oysters were taken only at Ward Point and their soft body tissues were decidedly green.

Shell and Weight Measurements

Table 1 summarizes the mean, standard deviation, and number of clams for all measurements of clam shell dimensions, weights, and percent solids taken during the study. Values for Ward Point were consistently lower than those for Horseshoe Cove or New Dorp Beach where the values were similar to one another. Student's "t" test revealed no significant difference in measurements between Horseshoe Cove and New Dorp Beach ($P > 0.05$), but a significant difference in all measured parameters was found between clams sampled in these areas and at Ward Point ($P < 0.01$) (Table 2).

Age Observations

For Ward Point, age determinations were made for the 5 smallest (collected 13 January 1975), the 5 largest specimens (collected 19 June 1974), and 8 specimens (collected 24 April 1974) which approximated the overall mean shell length. For New Dorp Beach, similar determinations were made for the 5 smallest (collected 21 February 1974), the 5 largest (collected 22 May 1974), and 13 specimens (collected 1 October 1974) which approximated the overall mean shell length. Some shells in the 24 April 1974 Ward Point and 1 October 1974 New Dorp Beach samples were not prepared for age determination, because severe shell erosion at the umbonal area indicated that early age lines would be incomplete.

Two differences were apparent. Firstly, none of the clams from Ward Point was older than 14 years, whereas clams at New Dorp Beach were as old as 20 years. Secondly, clams at Ward Point on

TABLE 1.—Measurements of the shell and meats of Raritan Bay hard clams, *Mercenaria mercenaria*, collected in 1974 and 1975.

	Sample locations								
	Ward Point			New Dorp Beach			Horseshoe Cove		
Measurements	Mean	SD	No.	Mean	SD	No.	Mean	SD	No.
Shell length (mm)	77.3	9.1	221	88.2	12.7	225	87.0	13.2	230
Shell height (mm)	64.6	9.8	221	74.5	11.0	225	72.6	12.7	230
Shell width (mm)	44.8	5.4	221	50.3	7.5	225	50.6	10.1	230
Shell dry wt (g)	95.0	29.5	201	136.2	48.9	225	138.1	48.7	230
Underwater wt (g)	51.4	15.0	221	74.6	26.7	225	77.6	31.3	230
Drained meat wt (g)	1.3	14.1	201	56.9	18.1	205	55.0	20.9	210
Dry meat wt (g)	5.9	2.1	201	9.0	3.5	205	9.1	4.0	210
Percent solids	14.3	3.2	201	15.8	3.7	205	16.5	3.9	210

TABLE 2.—Results of "*t*" *test comparing measurements of Raritan Bay hard clams, Mercenaria mercenaria*, collected in 1974 and 1975.

Measurements	Sample locations compared		
	Horseshoe Cove and Ward Point	New Dorp Beach and Ward Point	Horseshoe Cove New Dorp Beach
Shell length (mm)	9.0313**	10.3795**	0.9857
Shell height (mm)	7.4520**	10.0069**	1.7005
Shell width (mm)	7.5447**	8.8542**	0.3583
Shell dry wt (g)	10.8928**	10.3523**	0.4143
Underwater wt (g)	11.2380**	11.2120**	1.1330
Drained meat wt (g)	7.7373**	9.6513**	0.9866
Dry meat wt (g)	10.0644**	10.7691**	0.2701
Percent solids	6.2215**	4.3548**	1.8704

** – Highly significant ($P < 0.01$).

average were smaller at each age than those at New Dorp Beach (Fig. 2).

Reproductive Cycle

This part of the study focused on a microscopic examination of the cellular events leading up to an accumulation of sex cells in the gonads and their disappearance during the spawning act. Periodic sampling identified the time and duration of spawning. Cellular structures within the sex cells and alveoli walls were important in determining five stages of gonadal condition, as follows:

Females

Early stage. Alveoli semicontracted, basement membrane thickened, and small oocytes embedded in the alveoli walls.

Late stage. Oocytes more numerous at the basement membrane, some of larger diameter extended into the lumina of alveoli, but attached to

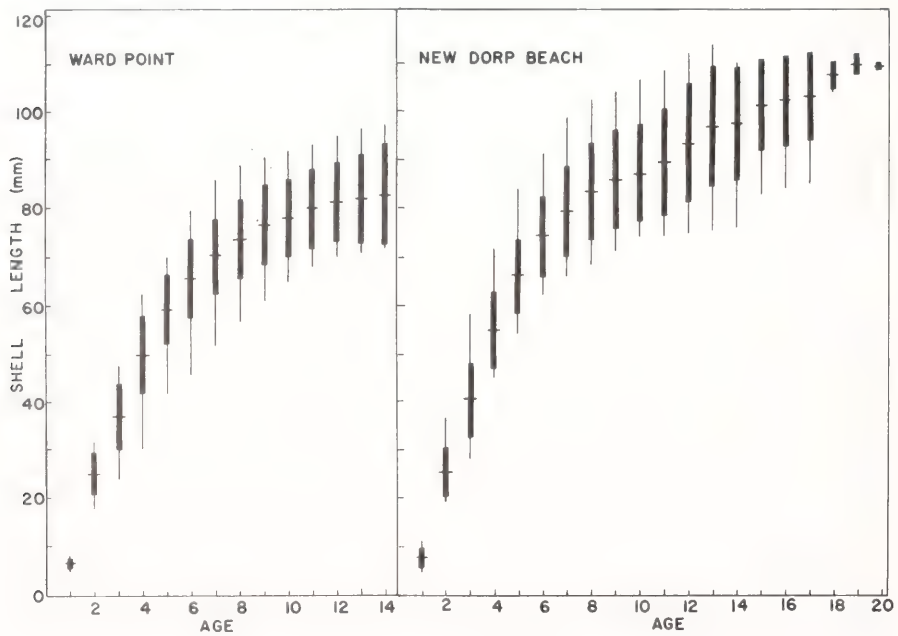

FIGURE 2.—Mean, standard deviation, and range of shell lengths (mm) vs. age (yr) relationships of hard clams, *Mercenaria mercenaria*, at Ward Point and New Dorp Beach, Raritan Bay, 1974-75.

the thickened basement membrane by a stalk. A few of the largest oocytes appear free in the lumina of alveoli. Amphinucleoli prominent in the largest oocytes.

Ripe stage. Numerous large oocytes in the lumina of alveoli. Basement membrane thin, containing only a few developing oocytes. Most oocytes appear free in the lumina of alveoli.

Partially spent stage. Some small oocytes embedded in the basement membrane, with reduced numbers of large oocytes in the alveoli lumina.

Spent stage. A very few of the largest oocytes in some of the alveoli lumina. Basement membrane somewhat thickened and containing small embedded oocytes.

Males

Early stage. Alveoli semicontracted, basement membrane thickened, and follicle cells prominent in the lumina. A few spermatogonia or spermatocytes occur at the periphery of the lumina in most clams, but some with a few spermatozoa scattered in the lumina of some alveoli.

Late stage. Alveoli expanded, basement membrane thin and attached follicular cells less apparent. Primary spermatocytes numerous at the basement membrane, especially during the earliest part of this stage. Secondary spermatocytes and spermatids proliferating into the centers of the lumina. Differentiated spermatozoa arranged in dense radiating bands at the centers of the lumina.

Ripe stage. Lumina of alveoli densely packed with spermatozoa. Fewer spermatocytes and spermatids occurring than in the preceding stage.

Partially spent stage. Few to no spermatocytes or spermatids at the basement membrane. Relatively reduced numbers of spermatozoa in the lumina of alveoli compared to the ripe stage.

Spent stage. Alveoli nearly empty of spermatozoa, but a few near the basement membrane and in the lumina.

For all three sites, gametogenesis progressed from the early to late stages from 21 February to 24 April 1974 (Table 3). Ripening was earliest at Horseshoe Cove, with 10% of the clams in this condition by 22 May and 70% by 19 June. At this latter date, 50% of the Ward Point clams were ripe. Clams at all the sites had ripened by 23 July, and some (20%) at Ward Point and many (70%) at New Dorp Beach were in the partially spent condition, an indication that spawning had begun at these two sites. Spawning was later at Horseshoe Cove, with 67% in the partially spent condition by 21 August. Ripe clams were observed in the sam-

TABLE 3.—Percent occurrence of developmental stages during the reproductive cycle of Raritan Bay hard clams, *Mercenaria mercenaria*, collected in 1974 and 1975.

	1974									1975		
Sample site and gonad condition	2 21	3 28	4 24	5 22	6 19	7/23	8 21	10 1	11 5	1/13	2 6	4 7
Horseshoe Cove												
early	60	70	30	40	10						40	100
late	40	30	70	50	20							
ripe				10	70	100	33	40	30			
part. spent							67	20	60	60		
spent								40	10	40	60	
New Dorp Beach												
early	70	70	70	50							80	90
late	40	20	30	50	100							
ripe						30	30					
part. spent						70	70	50	90	20		
spent		10						50	10	80	20	10
Ward point												
early	40	40	50	40							60	50
late	50	40	50	60	50							20
ripe					50	80	30	30				
part. spent						20	30	50	100			
spent	10	20					40	20		100	40	30

ples from Horseshoe Cove as late as 5 November, but only until 1 October and 21 August at Ward Point and New Dorp Beach, respectively. Partially spent clams were collected from Horseshoe Cove and New Dorp Beach as late as 13 January 1975, but only until 5 November 1974 at Ward Point. The spent and early gametogenic stages identified in clams from all sites by 6 February 1975 indicated that the 1974 reproductive cycle had been completed by all clams and that a new cycle had begun for some. These observations suggest that the spawning period was shortest at Ward Point (5 months) and longest at New Dorp Beach (7 months), with Horseshoe Cove intermediate (6 months).

At all three sites, gametogenesis progressed through morphologically normal stages resulting in the complete spawning of most ripe gametes. Cytolysis of unspent cells was not observed. No hermaphrodites were seen in any of the samples.

The sex ratios of hard clams in the samples were as follows: at Ward Point, 59 males and 60 females; at New Dorp Beach, 56 males and 64 females; and at Horseshoe Cove, 74 males and 45 females. The hypothesis of 1:1 sex ratio was tested by chi-square for all three populations; results indicated a significant ($P < 0.01$) deviation for Horseshoe Cove.

Histochemical Tests for Metals

Histochemical tests were performed on four male and six female hard clams and one male and one female oysters collected at Ward Point; and three male and seven female hard clams collected at New Dorp Beach. The expected histochemical reactions for metals in clam tissues were not observed, i.e., deep Prussian blue for inorganic iron, green granular precipitate for arsenites and arsenates, yellow opaque crystals or scarlet red precipitate by the chromate or rhodizonate methods, respectively for lead, and deep greenish-black precipitate for copper. Thus, the tests for metals in hard clam tissues proved to be negative. Female gonadal tissues tested for arsenites and arsenates from both collecting sites had 1-2 μm diameter granules in the oocyte cytoplasm but the color could not be determined. No similar granules were seen in male tissues. For the two oysters from Ward Point, the deep greenish-black precipitate for copper was evident in connective tissue cells beneath the body wall and palps (a similar reaction was also seen in the epidermal cells of the palps), around the digestive diverticula (Fig. 3), and near the base of cells lining the gills and gut. The connective tissue cells surrounding the male oyster gonadal tubules also tested positive. No similar reaction was seen in the connective tissue cells surrounding the female oyster gonadal tubules, which contained large and apparently normal oocytes. Although not seen in New Dorp Beach hard clam tissues, some gill tissues of hard clams from Ward Point tested for copper showed a slight darkening, but a precipitate was not clearly evident, such as was seen in oysters. The darkening was also absent in underlying connective tissue cells and other tissues. Modification of the technique to intensify the copper reaction was negative for all hard clam and oyster tissues from the two collection sites.

Discussion

Shell dimensions and shell and body weights clearly indicated a smaller size for hard clams at Ward Point than at New Dorp Beach and Horseshoe Cove, which was reflected in the age estimates. Clams at Ward Point were younger (none >14 years) and smaller ($\bar{X}$ = 77 mm; none >97 mm) than clams at New Dorp Beach (none >20 years; $\bar{X}$ = 88 mm; none >113 mm). These are values much lower than the 111 mm mean and maximum length of 144 mm reported for Nantucket Sound hard clams by Ropes and Martin (1960) and recent, almost 60-yr longevity estimate for the species (Ropes pers. obs.).

Determination of the percentage solids for the meats of bivalves is a measure of condition (Engle and Chapman 1953). The following mean values have been reported: 18.4% for soft-shell clams, *Mya arenaria* (Harriman 1954), 17.0% for oysters, *C. virginica* (Engle 1958), 21.4% for surf clams, *Spisula solidissima* (Barker and Merrill 1967), and 18.5% for ocean quahogs, *Arctica islandica*, (Ropes 1971a). These compare favorably with 16.5% and 15.8% for Horseshoe Cove and New Dorp Beach hard clams, respectively (Table 1). The low value of 14.3% for Ward Point hard clams is an indication of poor condition.

Reported age and growth determinations for hard clams suggest that the Ward Point portion of the Raritan Bay population was being adversely affected. Ansell (1968) has extensively reviewed the literature on annual and seasonal growth of hard clams from various investigations in Canada, the United States, and Europe. Length-on-age observations of the growth of hard clams at sites in Florida, North Carolina, New Jersey,

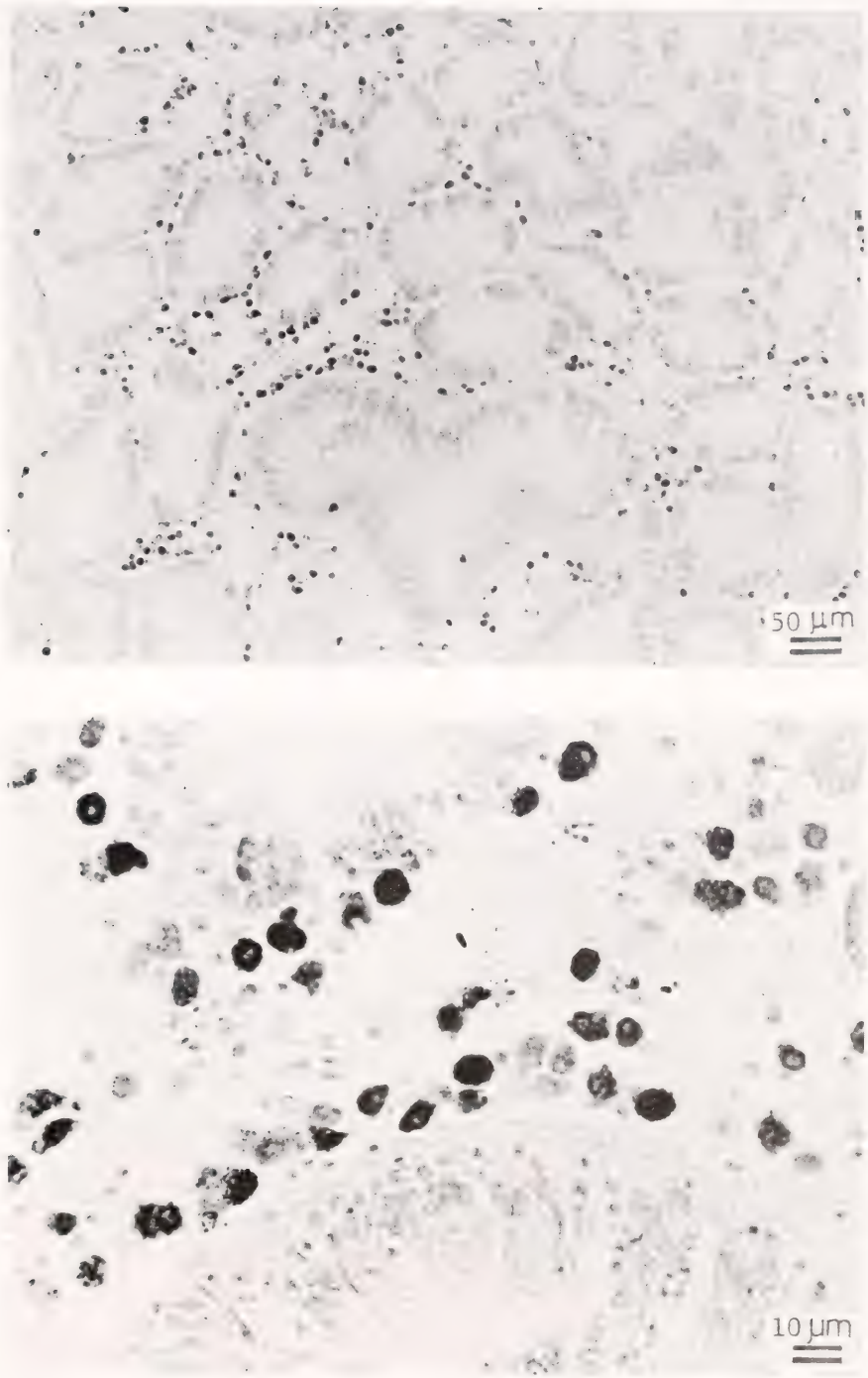

FIGURE 3.—Digestive diverticula of a copper "sick" oyster, *Crassostrea virginica*, from Raritan Bay. Connective tissue cells surrounding the diverticula were greenish black, a positive reaction of copper by the rubianic acid method. A scale of magnification appears in the lower right-hand corner of each photomicrograph.

New York, Massachusetts, Maine, and Canada were compared with the data for the hard clams sampled at the New Dorp Beach and Ward Point, Raritan Bay sites. Growth of Raritan Bay clams was about midway between the fastest (Florida) and the slowest (Canada). At Ward Point, growth to age 4 was about equal to New Jersey growth, but at New Dorp Beach, growth was consistently greater. After age 4, clams at Ward Point grew much slower than New Jersey clams, and even slower than Maine clams after age 5. These observations support the conclusion by Ansell (1968) of extreme local variations in the annual growth of hard clams.

The absence of large, old hard clams in the present samples may be the result of pollution effects, as Jefferies (1972) found for Providence River, RI, hard clams stressed by hydrocarbons. A high C_{15+} hydrocarbon value of 3,672 ppm in sediments at Ward Point was reported by Koons and Thomas (1979). Nevertheless, mortalities (e.g., paired valves containing dead bodies) were not evident at any site.

Food availability is considered an important factor for growth of hard clams by Ansell (1968). Jefferies (1962) considered the nutrient content of Raritan Bay to be rich and the environment capable of supporting dense biotic communities, because of a sluggish circulation pattern. Patten (1962) found that phytoplankton species diversity decreased up bay (towards Ward Point) from the higher values in the Lower Bay. A lower diversity of phytoplankton in the vicinity of Ward Point may have resulted in lower amounts of food organisms being available for the nutritional needs of the clams, and was probably reflected in their slower growth and poor meat condition.

Gonadal development culminated in spawning at three Raritan Bay sample sites. This suggests that the reproductive capacity of hard clams in Raritan Bay was not being affected by pollutants. However, some differences were noted in a comparison of the results based on available information about the time and duration of spawning and larval production at several northwestern Atlantic coast locations. At more northern locations, Belding (1912) and Deevey (1948) in Massachusetts, Landers (1954) in Rhode Island, and Carriker (1959, 1961) in Long Island, NY, and Little Egg Harbor, NJ, observed that spawning was initiated 1 to 2 months earlier than was observed in Raritan Bay during 1974. Similarly, at more southern locations, Keck et al. (1975) in Delaware, Sieling (1956) in Maryland, Ropes (1971b) and Chanley and Andrews (1971) in Virginia, Porter (1967) in North Carolina, and Eversole and Michner (1980) in South Carolina observed that spawning was initiated 1 to almost 3 months earlier. A spawning beginning about three-fourths of a month earlier than the present study was observed by Jefferies (1962) in Raritan Bay, but Loosanoff (1937) in Long Island, NY, observed that spawning began at the same time as in Raritan Bay during 1974. No particular trend in the time of peak spawning was evident in the several studies, except that the peak spawning in 1974 at all Raritan Bay sample sites was later than reported in any of the other studies. Spawning ceased somewhat earlier at more northern locations, and was not as prolonged at more southern locations as was observed in Raritan Bay during 1974.

The project was initiated under the premise that heavy metal pollution in Raritan Bay could be affecting the viability of adult hard clams. Studies indicated that tests for copper and lead should be specifically included, because high concentrations of both have been found in Raritan Bay sediment and water samples (Greig and McGrath 1977; Waldhauer et al. 1978).

The negative results of histochemical tests for heavy metals in Raritan Bay hard clams are not readily explained. Eisler (1981) has listed studies that found 15 heavy metals (including those tested for in the present study) in field collected hard clams. However, heavy metals can occur in several forms (Waldichuk 1979; Fayi and George 1985), suggesting that the histochemical tests may not have been specific for those occurring in Raritan Bay hard clams. Pringle et al. (1968) reported lower levels of copper in field collected hard clams than oysters (*Crassostrea virginica* and *C. gigas*). The positive result for copper in the oysters from Ward Point is probably related to the species greater sensitivity and accumulation of more of the metal in their tissues than hard clams. Copper may have been at a level too low for detection by the histochemical test, although limits for detection of copper or other metals were not given in Pearce (1972).

Hydrographic conditions (not specifically sampled for during the present study) probably influenced the growth and survival of hard clams in Raritan Bay. Based on current flow observed by Jefferies (1962) and Patten (1962), the New Dorp Beach area is influenced principally by water from the Hudson River and the ocean; the Ward Point area is influenced by an eddy formed from

the westward flow of water from the ocean, and flows from the Arthur Kill and Raritan Rivers; the Horseshoe Cove area is affected most strongly by water flowing from the Shrewsbury River.

Ansell (1968) analyzed data from throughout the geographical range of adult hard clams to develop a relationship between temperature and growth rate. Shell growth occurred between temperatures of 9°-31°C and ceased at lower and higher temperatures; the optimum was 20°C. Castagna and Chanley (1973) reported a salinity tolerance range of 12.5-46‰ for survival of adult hard clams, with an optimum of 24-28‰.

The above temperature and salinity limits for adult hard clams were compared with hydrographic results reported by Jefferies (1962). He listed mean surface and bottom water data beginning in summer 1957 to summer 1958 at two locations (Stations 1 and 6) in Raritan Bay near the Ward Point and New Dorp Beach sample sites, respectively. Throughout Raritan Bay no growth of adult clams would be expected during winter due to low bottom temperatures (2.3°-3.0°C); slow growth would occur during the increasing and decreasing temperatures of the spring and fall. Near normal growth probably occurs at New Dorp Beach and Ward Point during the summer when temperature means appeared to be near optimum conditions. Lowest bottom salinities were recorded during the spring at Jefferies' (1962) station number 1 near Ward Point. These values indicate that the minimum salinity tolerance limit for adult hard clams may occasionally be reached in the area. Salinities near the New Dorp Beach area (Jefferies 1962, station 6) were all within the tolerance limits for adult hard clams.

Jefferies (1962) reported dissolved oxygen measurements and found relatively low concentrations in the water near Ward Point in both summer periods. Slightly higher values occurred in the fall of 1957 and following spring near Ward Point, but the confidence intervals were greater than for any other period, indicating more variable conditions. Dissolved oxygen levels near New Dorp Beach were consistently higher than near Ward Point.

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ERRATA

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Utter, Fred, David Tell, George Milner, and Donald McIsaac, "Genetic estimates of stock compositions of 1983 chinook salmon, *Oncorhynchus tshawytscha*, harvests off the Washington coast and the Columbia River," p. 13–23.

Page 16, Table 1, Stock group, correct to read as follows:

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MORPHOMETRIC VARIATION OF PACIFIC OCEAN PERCH, *SEBASTES ALUTUS*, OFF WESTERN NORTH AMERICA

JAY C. QUAST[1]

ABSTRACT

Pacific ocean perch, *Sebastes alutus*, vary in body form over the eastern Pacific Ocean and southeastern Bering Sea. When related to a 260 mm standard length, a small adult size, most of 18 body measurements change from east to west as V-shaped clines. Belly size, however, lengthens as a single cline from the Vancouver vicinity westward, and the lengthening is coupled with shortening of measurements complementary to the belly measurement, from head to belly and belly to tail. Most adult body dimensions are sexually dimorphic, but the dimorphism is slight. Growth inflections may occur but, if so, are hidden in the data. Body form does not change markedly with growth except for the symphyseal knob, which becomes relatively larger, and the 3d anal-fin spine, which becomes relatively shorter. Putative subspecies of *S. alutus* probably are premature because supportive morphometric comparisons and criteria on the subspecies seem based on too few data, and do not adequately consider complex clinal variation and growth allometry evidenced in the eastern part of the species range. Also, significant morphometric variation may be phenotypic.

Pacific ocean perch, *Sebastes alutus*, a commercially important rockfish (Scorpaenidae) in the North Pacific Ocean, range from northern Honshu, Japan, to California. To date, the species' taxonomy has been based on relatively limited local representation, on preserved material, and on analyses without probabilistic interpretation or attention to allometric growth. Matsubara (1943) identified a Honshu representative as a new species (*Sebastes paucispinosus*), but Barsukov (1964), after examining specimens taken across the North Pacific Ocean, suggested that the variation he found indicated, at most, possible eastern and western Pacific subspecies, with both possibly occurring off the Aleutian Arc. Chen (1971) demonstrated that growth rate, can influence body proportions in a *Sebastes* species, and Westrheim (1973) found a cline of increasing growth rate in *S. alutus* from the northern Gulf of Alaska to Washington (Quast[2] found that the cline may be more related to latitude than temperature).

Because of the commercial importance of Pacific ocean perch and the lack of definitive information on possible subspecies or genetic stocks at the onset of the study, the National Marine Fisheries Service gathered morphometric data on representatives from the Gulf of Alaska and eastern Bering Sea from 1968 to the mid-1970's. We sought evidence of disjunct geographic variation that might indicate genetic stocks, and analyzed for characteristics of growth and sexual variation of possible taxonomic significance. Sampling was in the shallow range of the species distribution, at <200 fathoms (366 m).

METHODS

The prohibitively large volume needed for specimen storage for an extensive statistical study and the shrinkage, bending, and other distortions caused by preservation were avoided by photographing freshly trawled Pacific ocean perch. A portable stand supported a 35 mm camera and flash unit 145 cm above a V-shaped easel, which helped restrain the fish from vessel motion. The long focal distance minimized foreshortening in the photographs, and a 100 mm telephoto lens reduced field size to include only the specimen, a centimeter scale, a numbered theater ticket, and a plastic card with pencil-inscribed catch information. Specimens were flattened, straightened, and centered on the easel; fins were placed as erect as possible; and the lower jaw was propped closed with handheld forceps. Later, in the laboratory, body measurements were taken from images projected from the color transparencies onto the back of a ground-glass screen. The images

[1]Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821; present address: 1565 Jamestown Street S.E., Salem, OR 97302.

[2]Jay C. Quast. Annual growth in Pacific ocean perch, *Sebastes alutus*: variation, stanzas, compensation, and simulation. Manuscr. in prep.

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were brought to natural size by reference to the centimeter scale in each photograph. Accuracy was ensured for body-depth measurements by using a right-angle scale on the body axis.

The study used 18 linear measurements[3] (nearest millimeter) in addition to standard length (SL) of approximately 1,500 specimens sampled from the Bering Sea and Gulf of Alaska during summers of 1968-70 (Fig. 1, Table 1). The measurements gave major dimensions of the body and accessory structures, similar to those standard in taxonomic studies (Hubbs and Lagler 1949):

Standard length.—From tip of the premaxillary to the skin deflection (evidenced by a change in shading) at end of the hypural plate.

Nape.—From tip of premaxillary to the anterior insertion (junction of anterior outline with body profile) of the first spinous ray in the dorsal fin.

Spinous dorsal-fin length.—From anterior insertion of the spinous dorsal fin to the posterior insertion (junction of posterior outline of spine with body profile) of the 13th spinous fin ray.

Hind-trunk dorsal.—From posterior insertion of the 13th spinous fin ray to end of the hypural plate.

Hind-trunk ventral.—From posterior insertion of the second anal-fin spine to end of the hypural plate.

Belly.—From posterior insertion of the pelvic fin to posterior insertion of second anal-fin spine.

Pelvic insertion.—From tip of the premaxillary to posterior insertion of the pelvic fin.

Head.—From tip of the premaxillary to posterior edge of the opercular flap.

Body-depth pelvic.—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the posterior insertion of pelvic fin to dorsal body outline.

Body-depth anal.—Dorsoventral distance, taken perpendicular to the longitudinal axis of the fish, from the anterior insertion of first anal spine to dorsal body outline.

Caudal peduncle.—Shortest distance across caudal peduncle, taken perpendicular to its longitudinal axis.

Orbit.—Greatest diameter between opposite sides of the orbit, taken parallel to longitudinal axis

[3]Data for the measurements, including additional measurements not given in this paper, are available on tape as JQUAST/MORF1 on file at the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, 2725 Montlake Blvd. East, Seattle, WA 98112

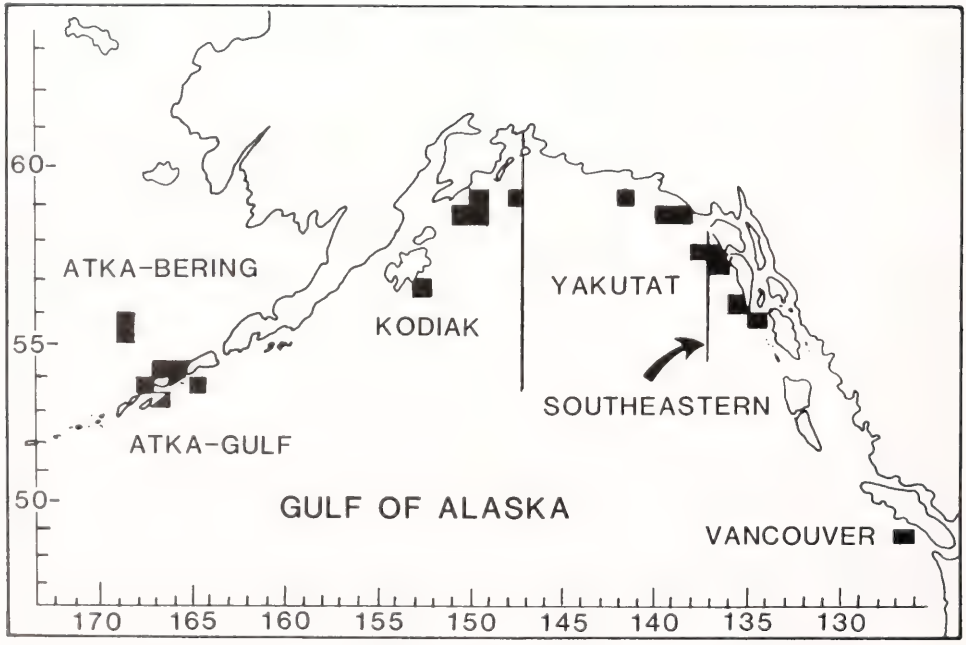

FIGURE 1.—Geographic regions and statistical areas (dark rectangles) where Pacific ocean perch were obtained for this study.

TABLE 1.—Standard-length (SL) frequencies of Pacific ocean perch used in this study. Geographic zones are shown in Figure 1. M = male; F = female.

Standard length (mm)		Atka-Bering		Atka-Gulf		Kodiak		Yakutat		South-eastern		Vancouver	
Class	Midpoint	M	F	M	F	M	F	M	F	M	F	M	F
115-134	125.5	5	5	—	—	—	—	—	—	—	1	—	—
135-154	145.5	3	4	—	1	—	—	—	—	—	1	—	—
155-174	165.5	4	5	1	—	4	4	—	—	1	2	—	—
175-194	185.5	16	14	2	4	14	15	2	5	4	5	—	—
195-214	205.5	20	15	13	9	6	7	4	11	15	7	—	—
215-234	225.5	13	26	51	55	10	6	16	24	13	8	—	—
235-254	245.5	36	22	49	52	6	7	14	19	7	5	5	—
255-274	265.5	22	19	25	12	7	8	9	10	12	17	4	2
275-294	285.5	16	22	15	13	19	9	4	10	16	9	10	4
295-314	305.5	10	13	26	21	65	33	6	7	23	5	13	3
315-334	325.5	17	25	13	22	16	35	4	8	11	5	9	4
335-354	345.5	3	26	1	7	4	18	4	4	—	—	2	8
355-374	365.5	3	17	—	1	—	2	1	5	—	1	2	1
375-394	385.5	—	2	—	—	—	—	2	—	1	—	—	1
395-414	405.5	—	—	—	—	—	—	—	—	1	—	—	1
Total by sex:		168	215	196	197	151	144	66	103	104	66	45	24
Region totals:		383		393		295		169		170		69	
Average SL, by region:		260.5		257.9		281.4		261.5		261.2		308.4	
Average SL, all data[1]:		266.41 (N = 1,479)											

[1]Class midpoints weighted by frequency.

of the fish.

Longest pectoral-fin ray.—From tip of the longest ray to its origin.

Upper-jaw length.—Greatest distance from tip of the premaxillary to posterior edge of the maxillary.

Upper-jaw width.—Greatest width of this part taken perpendicular to axis of the mouth line in a closed mouth.

Symphyseal knob.—From tip of symphyseal knob to its posterior insertion.

6th dorsal spinous fin ray.—From tip of this fin ray to its posterior insertion.

13th spinous ray in dorsal fin.—From tip of this ray to its posterior insertion.

3d anal-fin spine.—From tip of this spine to its posterior insertion.

The data were divided into six geographic regions (Atka-Bering, Atka-Gulf, Kodiak, Yakutat, Southeastern, and Vancouver (Fig. 1)), and measurements regressed on SL by sex after all variates were $\log_{10}$ transformed. (Transformation allowed measurements to be expressed as linear functions of SL and stabilized the variance.) Geographic and sexual variation were tested by analysis of covariance (ANCOVA), with statistical tests "significant" when $P \leq 0.05$.

In "allometric" growth in fishes, the size of one variate bears a power relationship to an index of body length. The power exponent can be expressed as the slope of a simple linear regression fit to log-transformed variates, the "allometric equation", as used in this study. A slope greater than unity, "positive allometry" (Simpson et al. 1960), indicates that growth in a body dimension relative to growth in fish length (SL in the present paper) increases as fish length increases; a slope less than unity, "negative allometry", indicates that growth in a body dimension decreases; and a slope of unity, "isometry", indicates that it stays the same.

A preliminary survey of the measurement data disclosed that most body dimensions probably grow allometrically, although not strongly so because slopes are near unity (Table 2). Because body proportions that relate size of a character to SL are specific to body length when growth is allometric, both proportions and dimensions must be referred to a size standard if either are to be objectively compared. For this reason, measurements and proportions used here are usually referred to a hypothetical fish of 260 mm SL, a size near the average for all specimens in the study (Table 1), and likely a common collection size. In most instances, body proportions represented by estimated dimensions at the standard size need not be limited to exactly that size for purposes of general comparison because of the proximity of allometric slopes to unity (Table 2). The data

TABLE 2.—Parameters for linear regressions (data $\log_{10}$ transformed) of measurements on standard length (mm) for Pacific ocean perch sampled from the Bering Sea (Atka-Bering region) to Vancouver Island, British Columbia. Slopes in italics are significantly different from one ($P \leq 0.05$). ANCOVA indicates significance of tests for geographic variation over the six zones by analysis of covariance (if slopes tested significantly different, intercepts were not tested).

	Males				Females			
Region	*N*	Intercept	Slope	R^2	*N*	Intercept	Slope	R^2
			NAPE					
Atka-Bering	168	−0.57942	*1.04767*	0.986	215	−0.54925	*1.03434*	0.988
Atka-Gulf	196	−0.49916	1.01264	0.946	197	−0.59329	*1.05137*	0.964
Kodiak	150	−0.52788	*1.02511*	0.984	144	−0.50253	1.01401	0.989
Yakutat	66	−0.52515	1.02721	0.965	102	−0.37849	0.96596	0.960
Southeastern	103	−0.52149	*1.02716*	0.984	65	−0.31086	*0.92727*	0.983
Vancouver	45	−0.60283	1.06479	0.957	24	−0.55937	1.04431	0.947
ANCOVA		—	***			—	***	
			SPINOUS DORSAL-FIN LENGTH					
Atka-Bering	168	−0.46575	1.00808	0.970	215	−0.51738	*1.03007*	0.984
Atka-Gulf	196	−0.48033	1.01155	0.938	197	−0.53388	*1.03434*	0.950
Kodiak	151	−0.40715	0.98179	0.968	144	−0.47812	1.01100	0.937
Yakutat	65	−0.41767	0.98430	0.945	103	−0.60298	*1.06233*	0.939
Southeastern	104	−0.65332	*1.07876*	0.965	66	−0.66303	*1.08146*	0.975
Vancouver	45	−0.18623	*0.88693*	0.887	24	−0.46602	1.00011	0.895
ANCOVA		—	***			***	NS	
			HIND-TRUNK DORSAL					
Atka-Bering	168	−0.34928	*0.96296*	0.977	213	−0.31407	*0.94808*	0.981
Atka-Gulf	196	−0.43921	1.00161	0.932	197	−0.34965	*0.96475*	0.958
Kodiak	151	−0.52480	*1.03743*	0.977	144	−0.49997	1.02683	0.973
Yakutat	65	−0.48155	1.01525	0.965	103	−0.48653	1.01744	0.955
Southeastern	104	−0.31689	*0.94900*	0.976	66	−0.55759	*1.05007*	0.978
Vancouver	45	−0.43589	0.99412	0.900	24	−0.52323	1.02901	0.930
ANCOVA		—	***			—	***	
			HIND-TRUNK VENTRAL					
Atka-Bering	168	−0.36545	*0.95394*	0.976	215	−0.17229	*0.86822*	0.970
Atka-Gulf	196	−0.36803	0.95720	0.908	197	−0.15326	*0.86477*	0.908
Kodiak	151	−0.30535	*0.93808*	0.928	144	−0.14297	*0.86656*	0.942
Yakutat	65	−0.21169	*0.89828*	0.900	103	−0.10019	*0.84914*	0.872
Southeastern	104	−0.36519	*0.96875*	0.978	66	−0.30279	*0.94197*	0.980
Vancouver	45	−0.15815	*0.88163*	0.942	24	−0.06116	*0.79192*	0.804
ANCOVA		***	NS			***	NS	
			BELLY					
Atka-Bering	168	−0.37364	*0.94635*	0.956	215	−0.70418	*1.09162*	0.965
Atka-Gulf	196	−0.33800	*0.92788*	0.808	197	−0.62569	*1.05150*	0.906
Kodiak	151	−0.60457	1.02908	0.832	144	−0.85483	*1.14125*	0.909
Yakutat	63	−0.97655	*1.17854*	0.880	97	−1.03204	*1.20777*	0.872
Southeastern	102	−0.61599	1.01693	0.903	66	−0.83303	*1.11490*	0.919
Vancouver	45	−0.81199	1.10045	0.802	24	−1.13734	*1.24044*	0.862
ANCOVA		—	***			—	*	
			PELVIC INSERTION					
Atka-Bering	168	−0.55435	*1.06386*	0.988	215	−0.46702	*1.02686*	0.988
Atka-Gulf	196	−0.51060	*1.04589*	0.958	197	−0.55050	*1.06143*	0.976
Kodiak	151	−0.43680	1.01440	0.973	144	−0.44339	1.01430	0.982
Yakutat	61	−0.40669	1.00918	0.961	97	−0.29310	0.95993	0.959
Southeastern	104	−0.40062	1.00887	0.970	66	−0.24953	*0.94551*	0.968
Vancouver	45	−0.53731	1.06759	0.944	24	−0.54122	1.06600	0.926
ANCOVA		—	*			—	***	
			HEAD					
Atka-Bering	167	−0.66929	*1.08599*	0.985	211	−0.54938	*1.03404*	0.986
Atka-Gulf	193	−0.62867	*1.06805*	0.956	95	−0.66243	*1.08088*	0.974
Kodiak	149	−0.58928	*1.04964*	0.974	141	−0.46700	0.99665	0.987
Yakutat	65	−0.56204	1.04073	0.961	103	−0.38096	0.96489	0.962
Southeastern	104	−0.52223	1.02793	0.979	65	−0.25528	*0.91393*	0.979
Vancouver	45	−0.45179	1.00443	0.935	24	−0.41197	0.98543	0.935
ANCOVA		—	*			—	***	

NS = $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.005$.

TABLE 2.—*Continued.*

Region	Males				Females			
	N	Intercept	Slope	R^2	*N*	Intercept	Slope	R^2
BODY-DEPTH PELVIC								
Atka-Bering	168	−0.51033	1.00257	0.976	215	−0.54783	*1.01989*	0.980
Atka-Gulf	196	−0.53594	1.00921	0.928	197	−0.69474	*1.07506*	0.951
Kodiak	151	−0.52962	1.00452	0.967	144	−0.62554	*1.04313*	0.982
Yakutat	65	−0.61821	1.04588	0.961	103	−0.55126	1.01765	0.946
Southeastern	104	−0.71748	*1.08660*	0.978	66	−0.64909	*1.05958*	0.982
Vancouver	45	−0.79012	*1.12032*	0.951	24	−1.02734	*1.21485*	0.973
ANCOVA		—	***			—	***	
BODY-DEPTH ANAL								
Atka-Bering	168	−0.31899	*0.88824*	0.970	215	−0.23926	*0.85418*	0.959
Atka-Gulf	196	−0.35517	*0.89788*	0.903	197	−0.31260	*0.87925*	0.930
Kodiak	150	−0.48843	*0.94820*	0.949	144	−0.48666	*0.94522*	0.972
Yakutat	66	−0.44835	0.93799	0.930	103	−0.46838	*0.94474*	0.933
Southeastern	104	−0.60709	1.00067	0.958	66	−0.69547	1.03764	0.960
Vancouver	45	−0.45563	0.94021	0.848	24	−0.47752	0.94904	0.769
ANCOVA		—	***			—	***	
CAUDAL PEDUNCLE								
Atka-Bering	168	−0.89038	*0.92634*	0.970	215	−0.75477	*0.86857*	0.964
Atka-Gulf	196	−0.96731	*0.95528*	0.932	197	−0.83252	*0.89772*	0.928
Kodiak	151	−1.03039	0.97784	0.954	144	−1.04643	0.98133	0.972
Yakutat	66	−0.90622	*0.93157*	0.947	103	−0.86913	*0.91426*	0.944
Southeastern	102	−0.98737	0.96392	0.958	66	−0.99718	0.97023	0.964
Vancouver	45	−0.86566	0.91611	0.818	24	−0.88816	0.92524	0.838
ANCOVA		—	***			—	***	
ORBIT								
Atka-Bering	168	−1.12729	1.03674	0.943	215	−0.97536	0.97242	0.949
Atka-Gulf	196	−1.02260	0.99192	0.793	197	−1.05490	1.00415	0.861
Kodiak	151	−1.07754	1.00791	0.802	144	−0.83433	*0.90505*	0.786
Yakutat	65	−0.89752	0.92381	0.866	102	−0.71441	*0.84725*	0.830
Southeastern	103	−1.16845	1.03324	0.899	66	−0.83621	*0.89158*	0.903
Vancouver	45	−0.14594	*0.62383*	0.862	24	−0.22779	*0.65647*	0.667
ANCOVA		—	***			—	**	
LONGEST PECTORAL-FIN RAY								
Atka-Bering	168	−0.64359	1.02265	0.970	215	−0.53922	*0.97618*	0.978
Atka-Gulf	196	−0.63481	1.01701	0.937	197	−0.51453	*0.96360*	0.948
Kodiak	151	−0.55655	0.98090	0.947	144	−0.44668	*0.93236*	0.961
Yakutat	66	−0.72067	1.04225	0.923	102	−0.61357	0.99762	0.942
Southeastern	101	−0.88825	1.12077	0.968	66	−0.78218	*1.07402*	0.956
Vancouver	45	−0.50319	0.96330	0.901	23	−0.73958	1.05622	0.934
ANCOVA		—	**			—	**	
UPPER-JAW LENGTH								
Atka-Bering	168	−1.07654	*1.10238*	0.947	215	−0.92793	*1.03735*	0.955
Atka-Gulf	196	−1.11966	*1.12050*	0.854	195	−1.04190	*1.08558*	0.910
Kodiak	151	−0.84319	1.00090	0.898	144	−0.65487	*0.91998*	0.932
Yakutat	64	−0.64407	0.91575	0.788	101	−0.57472	*0.88516*	0.770
Southeastern	104	−0.99592	1.06287	0.838	66	−0.81778	0.98171	0.819
Vancouver	45	−0.52744	0.86802	0.711	24	−0.16892	*0.72101*	0.651
ANCOVA		—	***			—	***	
UPPER-JAW WIDTH								
Atka-Bering	168	−1.37815	1.03050	0.891	215	−1.38585	1.02967	0.915
Atka-Gulf	196	−1.49225	1.07165	0.804	197	−1.41203	1.03808	0.838
Kodiak	151	−1.23784	0.96166	0.776	143	−1.20719	0.94924	0.880
Yakutat	66	−1.31512	1.00107	0.844	103	−1.20986	0.95659	0.839
Southeastern	104	−1.56596	*1.11473*	0.880	66	−1.00614	*0.87986*	0.881
Vancouver	45	−1.91421	*1.25943*	0.775	23	−1.81392	1.21350	0.748
ANCOVA		—	*			—	***	

NS $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.005$

TABLE 2.—*Continued.*

Region	Males				Females			
	N	Intercept	Slope	R^2	*N*	Intercept	Slope	R^2
SYMPHYSEAL KNOB								
Atka-Bering	166	−3.09541	*1.56992*	0.769	215	−2.81549	*1.44987*	0.814
Atka-Gulf	196	−2.80011	*1.43432*	0.540	197	−2.87970	*1.46848*	0.576
Kodiak	151	−3.82404	*1.87456*	0.876	144	−3.23909	*1.63193*	0.857
Yakutat	66	−3.01114	*1.52401*	0.785	103	−2.54090	*1.32784*	0.714
Southeastern	104	−2.53152	*1.32159*	0.808	65	−3.23953	*1.60663*	0.817
Vancouver	45	−2.90945	*1.47650*	0.638	24	−2.42106	1.28184	0.570
ANCOVA		—	***			***	NS	
6TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	167	−0.94686	1.00886	0.882	209	−0.79653	*0.94481*	0.900
Atka-Gulf	194	−0.99815	1.03241	0.735	191	−1.07166	1.05966	0.783
Kodiak	148	−0.82023	0.95342	0.836	136	−0.62671	*0.86982*	0.845
Yakutat	64	−1.19498	1.10184	0.818	97	−0.91257	0.98441	0.800
Southeastern	90	−1.17989	*1.10021*	0.894	59	−1.00276	1.02520	0.877
Vancouver	44	−0.64705	0.88566	0.616	19	−0.81268	0.94818	0.649
ANCOVA		***	NS			—	**	
13TH SPINOUS RAY IN DORSAL FIN								
Atka-Bering	165	−0.87157	*0.91366*	0.804	208	−0.72181	*0.85087*	0.834
Atka-Gulf	192	−0.98173	0.96415	0.621	183	−1.02884	0.98308	0.730
Kodiak	141	−0.85834	*0.91216*	0.766	133	−0.90253	0.92803	0.780
Yakutat	63	−0.94187	0.94260	0.771	87	−0.85833	0.90897	0.744
Southeastern	95	−0.79462	*0.88878*	0.816	57	−0.95486	0.95753	0.783
Vancouver	42	−0.39052	0.73692	0.394	20	−1.10477	1.01967	0.638
ANCOVA		***	NS			***	NS	
3D ANAL-FIN SPINE								
Atka-Bering	147	−0.50863	*0.81717*	0.849	190	−0.39317	*0.76948*	0.865
Atka-Gulf	166	−0.24648	*0.71104*	0.682	172	−0.18951	*0.68697*	0.696
Kodiak	131	−0.36994	*0.75870*	0.785	126	−0.32305	*0.73849*	0.818
Yakutat	62	−0.14422	*0.66714*	0.690	93	−0.45754	*0.79909*	0.714
Southeastern	66	−0.15004	*0.67029*	0.061	44	−0.54744	*0.82184*	0.742
Vancouver	40	+0.33516	*0.46515*	0.374	19	+0.28173	*0.48651*	0.451
ANCOVA		—	***			***	NS	

NS $P > 0.05$, $^{*}P < 0.05$, $^{**}P < 0.01$; $^{***}P < 0.005$.

agree with visual impressions of negligible proportional changes with growth, gained from working with the species in the field.

To compare measurement variability for sexual and geographic factors in untransformed data, in the section on character discrimination, I obtained symmetrical estimates of variation about mean values by taking limits formed by one standard deviation (about each regression by sex within region) on each side of the transformed means. I then back-transformed the limits and halved the difference between them. This symmetrical substitute for the asymetrical standard deviation about regression is called the "alternate standard deviation".

Westrheim (1975) studied sexual maturity in Pacific ocean perch from the Gulf of Alaska and concluded that onset occurred between 195 and 260 mm SL [fork length (FL) converted to SL by relationships established from the present morphometric data: SL=−3.272+0.879 FL, where N=1,528 and R^2=0.997]. In the present study, the boundary between juveniles and adults is taken as 230 mm SL.

Body Form Varied Geographically and by Sex

Although later, more detailed, analyses disclosed that the constant slopes required by the ANCOVA program BMDP P2V (Dixon et al. 1977) for each character (transformed data) were technically unmet, a preliminary analysis with this program indicated likely significant geographic and sexual variation in all characters (subsequently confirmed in detailed analyses with a more general ANCOVA model, Table 2), and a general lack of interaction between these factors. Also, I determined that only negligible bias has been induced in the regressions by logarithmic transformation of data by computing mean response variables, at 260 mm SL, for untransformed measurements fit by nonlinear least squares (BMDP PAR, Dixon et al. 1977). For six

measurements, by sex and region, over which the two methods were compared, the prediction of character sizes in fish of 260 mm SL by nonlinear least squares was close to the mean and within the 95% confidence interval for prediction from transformed data (Fig. 2) and did not change the results.

Graphical comparison of character measurements, related to the standardized fish of 260 mm SL, also disclosed that geographic and sexual variation were frequent:

Nape (Fig. 2A).—Geographic variation in distance between tip of snout and the dorsal fin was significant. Napes averaged shortest in the Atka-Gulf and Kodiak regions and lengthened in a cline to the Vancouver region. Females averaged smaller napes than males in all regions.

Spinous dorsal-fin length (Fig. 2B).—Geographic variation in length of spinous dorsal fin was significant, and the fin shortened in a cline from the Bering Sea to the Southeastern and Vancouver regions. Because geographic variation in length of the spinous dorsal fin was nearly opposite to geographic variation in the nape, changes in position of the anterior fin insertion probably caused the reciprocal clines. Sexual dimorphism was not important.

Hind-trunk dorsal (Fig. 2C).—Distance between the spinous dorsal fin and the tail changed significantly between regions. It averaged largest in specimens from the middle regions (Atka-Gulf and Kodiak) and smallest in the Vancouver region. Sexual dimorphism was not important.

Hind-trunk ventral (Fig. 2D).—Distance between the second spine of the anal fin and the tail changed significantly between regions. It averaged largest in the Southeastern and Vancouver regions and shortest in the Atka-Bering region. The data formed a geographic cline opposite to that of the belly measurement. From the Yakutat region westward, females averaged significantly shorter in this measurement than males.

Belly (Fig. 2E).—Distance between the pelvic fins and anal-fin spines varied significantly geographically and decreased in a cline from northwest to southeast (Atka-Bering region to the Southeastern and Vancouver regions). Belly measurements averaged about 1.6 cm smaller in the southeastern extreme of the sampling range than in the northwestern. The cline apparently is caused by opposing relational movements of pelvic girdle and anal-fin spines along the body axis because the pelvic insertion and hind-trunk ventral measurements decreased from southeast to northwest. Sexual dimorphism was significant, with bellies of males averaging about 4 mm smaller than those of females.

Pelvic insertion (Fig. 2F).—Geographic variation in distance between snout and pelvic fins was significant, and the distance increased from northwest to southeast, from the Atka-Bering region to the Vancouver region. The measurement averaged shorter in females than males in all regions, evidence for significant sexual dimorphism.

Head (Fig. 2G).—Geographic variation in head length was significant, and heads averaged shortest in the Kodiak region and longest in the Vancouver region. Sexual dimorphism was usually significant, and females averaged smaller heads than males. Trends in geographic and sexual variation between the head and pelvic insertion were similar, probably because both measurements include similar regions of the head.

Body-depth pelvic (Fig. 2H).—Geographic variation in body depth at the pelvic fins was significant and formed a broken cline. Deepest bodies occurred at the extremes of the sampling range (Atka-Bering and Vancouver regions), and were shallowest in the Kodiak region. Sexual dimorphism was inconsistent.

Body-depth anal (Fig. 2I).—Geographic variation in body depth at the anal spines was significant, and depth was shallowest in Kodiak specimens and deepest in Atka-Bering specimens. Body depths averaged smaller in females than in males from the Yakutat region to the Atka-Bering region, but the differences may not be significant.

Caudal peduncle (Fig. 2J).—Geographic variation in depth of caudal peduncle was significant, but important geographic differences were limited to regions west of Yakutat. Specimens from the Kodiak region averaged narrowest peduncles, and specimens from the Atka-Bering, Southeastern, and Vancouver regions averaged widest peduncles. Caudal peduncles averaged significantly narrower in females than in males except in the Southeastern and Vancouver regions.

Orbit (Fig. 2K).—Geographic variation in orbit diameter was significant. Diameters were

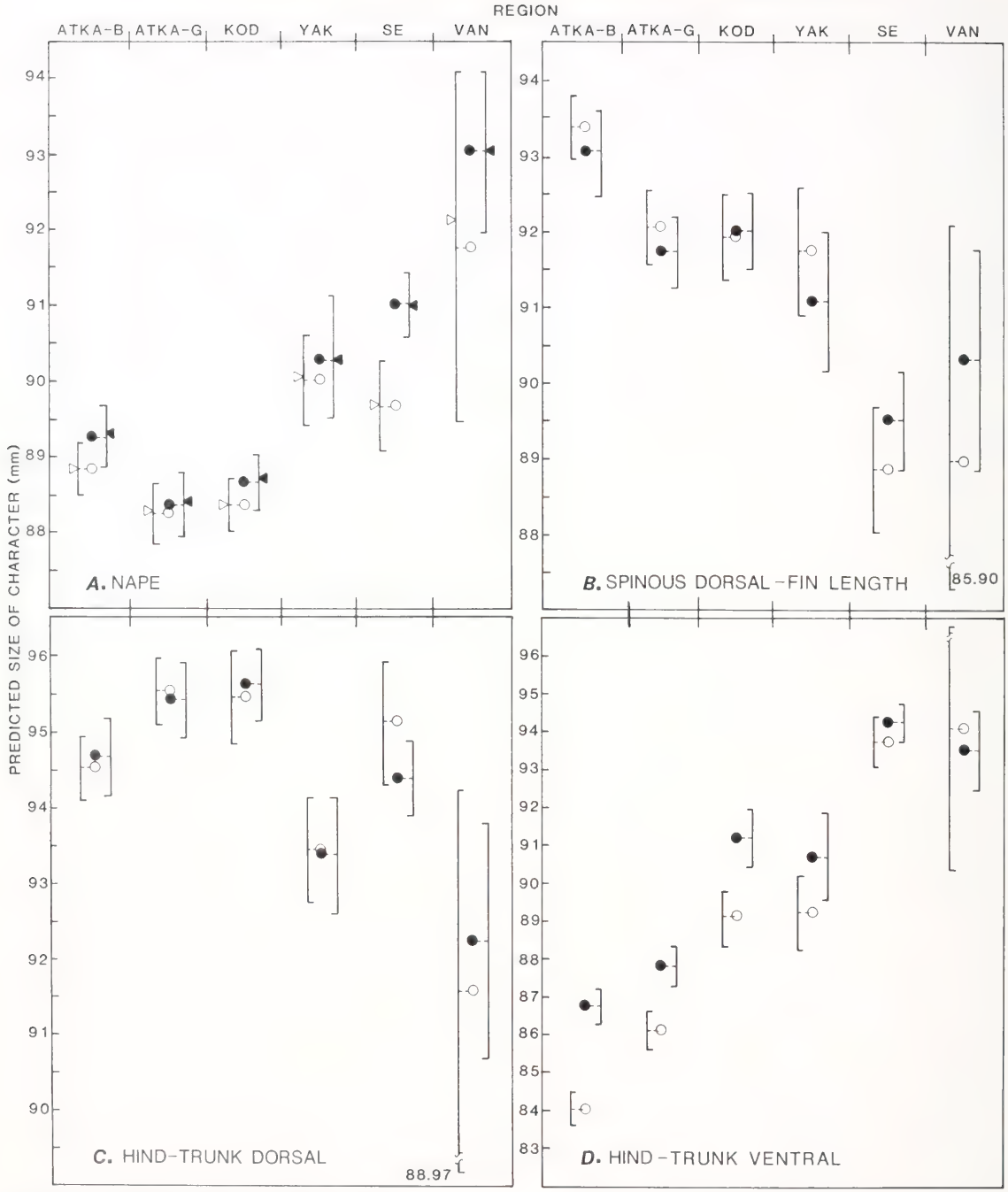

FIGURE 2.—Geographic and sexual variation in measurements of Pacific ocean perch in the northeastern Pacific Ocean and eastern Bering Sea as represented by mean responses to regression functions (Table 2) (circles) and 95% confidence intervals (brackets) for these responses as related to a standard-sized fish of 260 mm SL. Solid symbols represent males and open symbols females. Triangles represent mean responses by nonlinear least squares analysis (Dixon et al. 1977) for 260 mm SL fish.

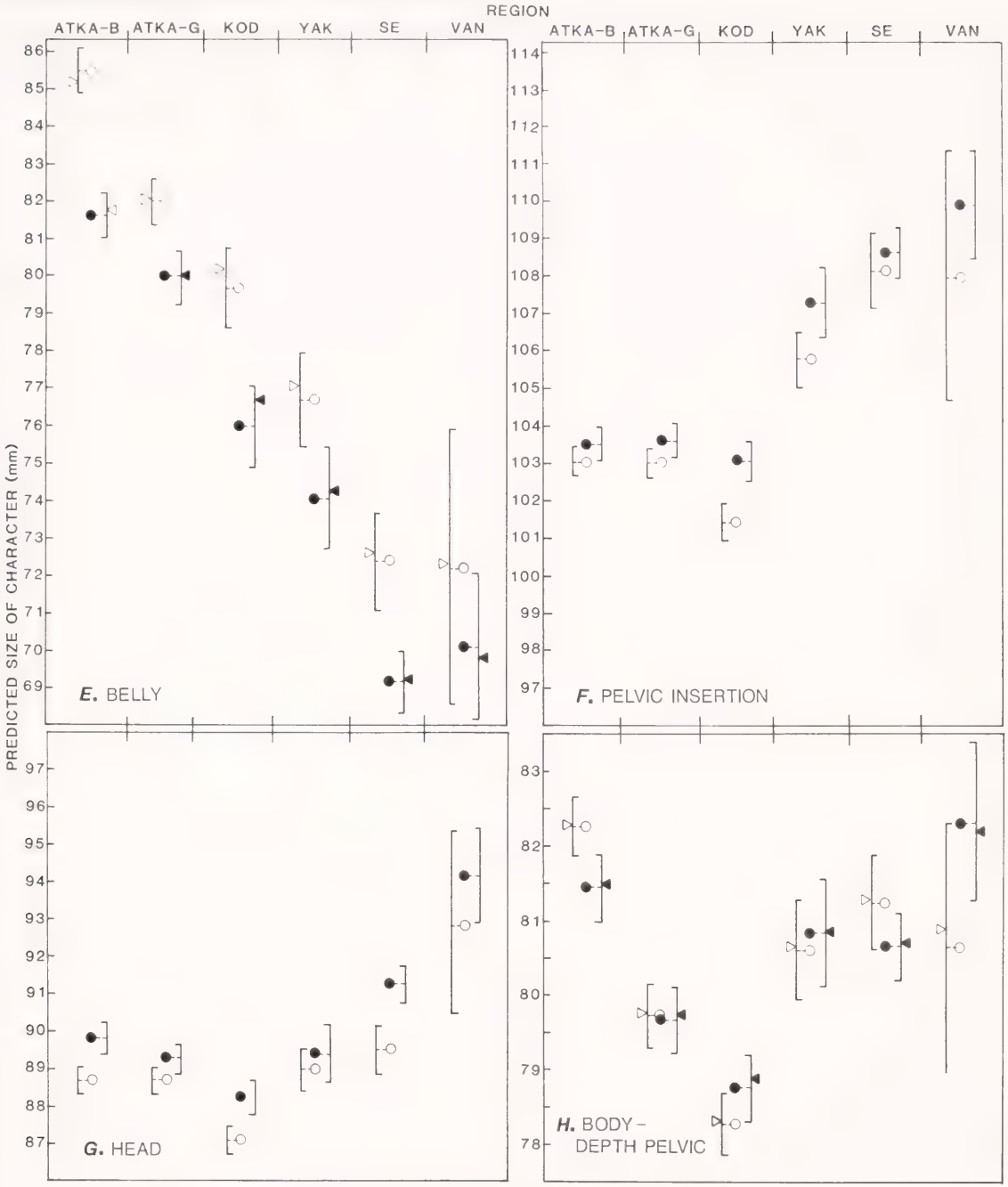

FIGURE 2.—*Continued.*

largest in the Atka-Bering and Atka-Gulf regions and smallest in the Southeastern region. Diameters decreased continuously from the Atka-Bering region to the Southeastern region, but the trend was broken by Vancouver samples. Although not significant within regions, sexual differences in orbit diameter probably were significant overall because females averaged smaller orbits than males in all regions.

Longest pectoral-fin ray (Fig. 2L).—Geographic variation in length of pectoral fins was significant. The fins averaged longest at the eastern

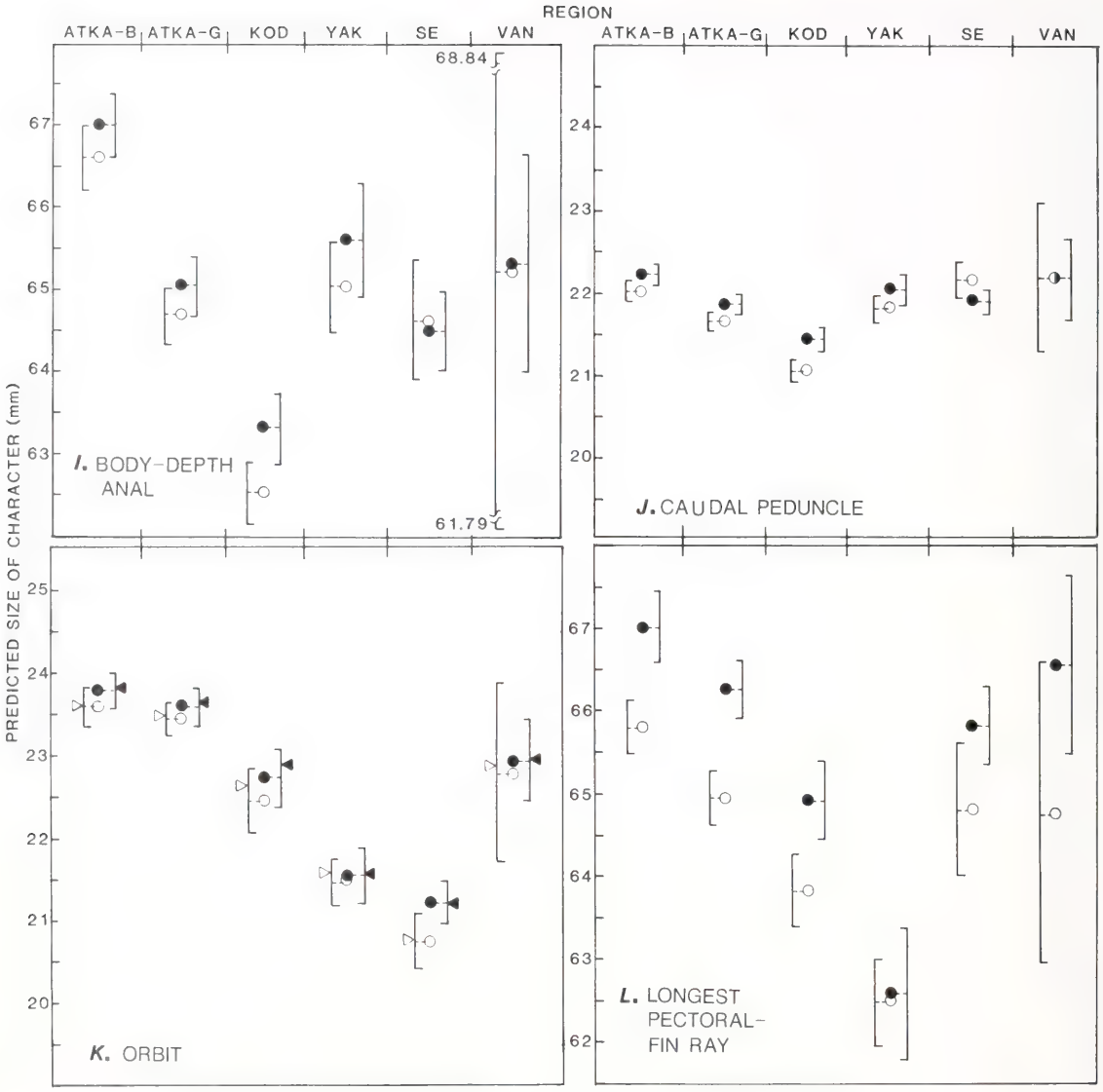

FIGURE 2.—*Continued.*

and western extremes of the sampling range and shortest in the Yakutat region. In all regions but Yakutat, sexual dimorphism was high and significant, and fins in females averaged >1 mm shorter than in males.

Upper-jaw length (Fig. 2M).—Geographic variation was significant, and jaws averaged longest in eastern Aleutian samples (Atka-Bering and Atka-Gulf regions). Sexual dimorphism was significant in three regions (Atka-Bering, Atka-Gulf, and Southeastern), with females averaging shorter upper jaws than males in each.

Upper-jaw width (Fig. 2N).—Geographic variation was significant, with upper jaws averaging narrowest in the Kodiak region. Sexual dimorphism was important in only the Atka-Bering and Southeastern regions, where females averaged narrower upper jaws than males.

Symphyseal knob (Fig. 2O).—Geographic variation was significant but erratic. On average, specimens from the Atka-Gulf region probably have the largest symphyseal knobs. Sexual dimorphism seems unimportant.

6th spinous ray in dorsal fin (Fig. 2P).—Geo-

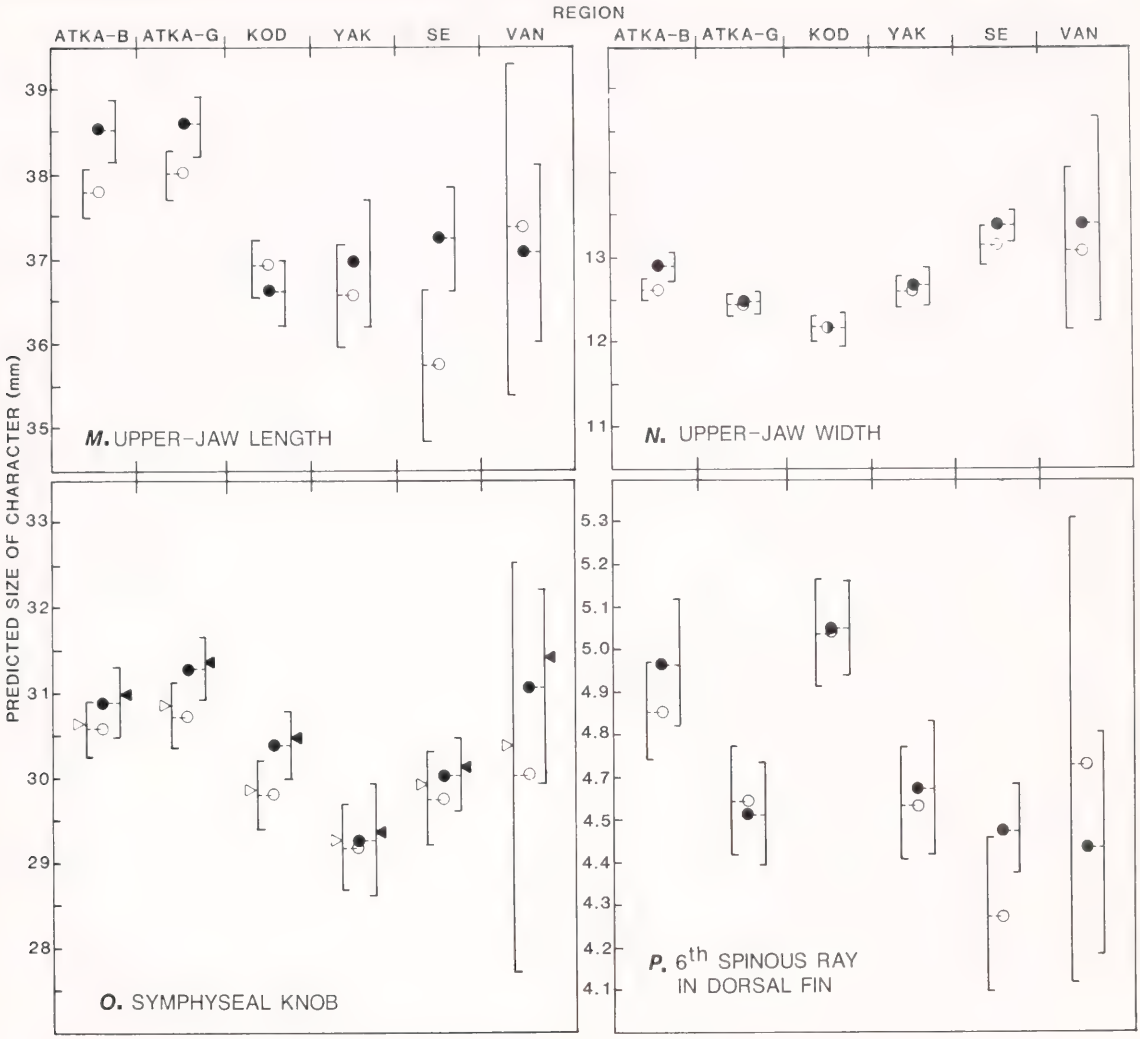

FIGURE 2.—*Continued.*

graphic variation was significant but erratic in this index to height of the spinous dorsal fin. Kodiak specimens had the highest spinous dorsal fins, on average. Sexual variation was inconsistent and is probably unimportant.

13th spinous ray in dorsal fin (Fig. 2Q).—Geographic variation was significant but erratic in this index to height of the notch between spinous and soft dorsal fins. Sexual dimorphism seems generally unimportant.

3d anal-fin spine (Fig. 2R).—Geographic and sexual variation in length of the spinous ray was minor, except that the fin spine was unusually short in females from the Southeastern region.

The measurements (as related to the standardized fish of 260 mm SL) usually varied geographically either in generally monotonic clines over the study area (Atka-Bering to Vancouver regions) or V-shaped clines that were broken in the Yakutat or Kodiak region. Only two sets of characters varied almost monotonically, and variation within each can be ascribed to a progressive shift in boundary features for body regions: Length of nape generally decreased and length of the spinous-dorsal fin increased from southeast to northwest (Fig. 2A, B), probably because of a relational shift in the dorsal-fin insertion. Belly size increased from southeast to northwest (Fig. 2E), probably because the pectoral girdle and associ-

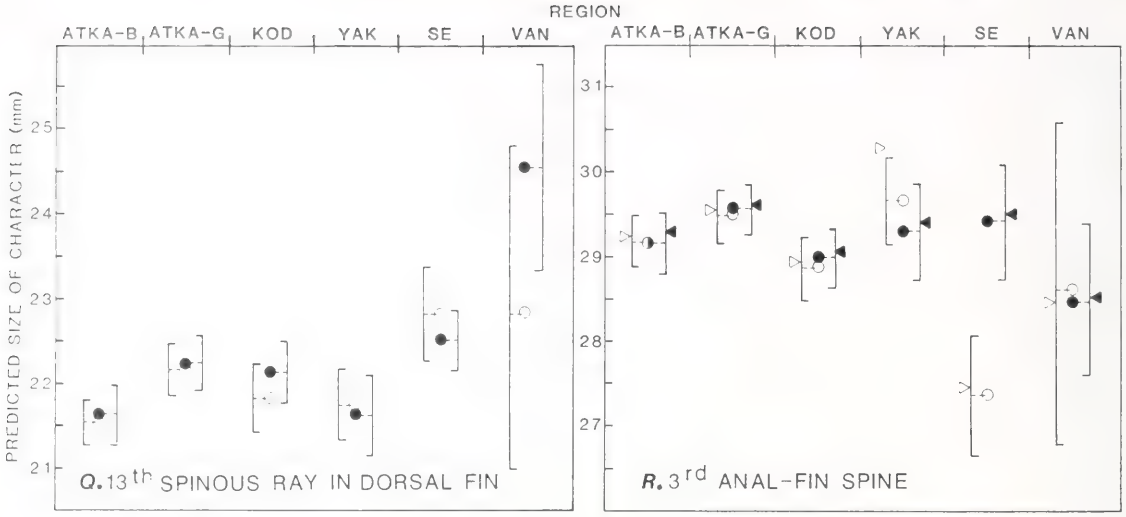

FIGURE 2.—*Continued.*

ated pelvic fins and the complex of anal-fin spines moved relationally apart (Fig. 2F, D). In contrast, depth of the entire body of Pacific ocean perch varied similarly geographically because the three measures of body depth—body-depth pelvic, body-depth anal, and caudal peduncle—varied concordantly (Fig. 3).

Sexual dimorphism was significant in most measurements, and except for belly size, measurements usually averaged larger in males than in females. The combined effects of geographic and sexual variation meant that belly measurements averaged about 16 mm larger in standard-sized females from the Atka-Bering region than in males from the Southeastern or Vancouver region (Fig. 2E).

Slopes in over one-half of the measurement regressions differed significantly from unity (Table 2), indicating growth allometry, particularly when differences from unity were consistent. The symphyseal knob was the only character with strong positive allometry (Table 2). Only two characters were strongly or consistently negatively allometric (Table 2): hind-trunk ventral, significant in 11 of 12 sex/region cells (slopes averaging 0.94 in males and 0.87 in females); and length of 3d anal-fin spine, significant in all 12 sex/region cells (slopes averaging 0.72 in males and 0.74 in females). With growth, the trunk posterior to the anal-fin spines becomes proportionally smaller relative to the rest of the body because of negative allometry in the body-depth anal, hind-trunk ventral, and caudal peduncle measurements.

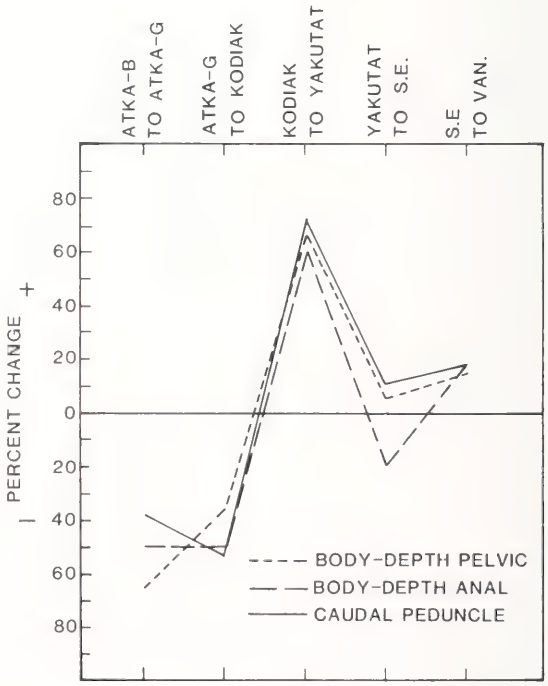

FIGURE 3.—Geographic variation in depth measurements of three body characters in Pacific ocean perch. Character measurements were related to a standard-sized fish of 260 mm SL from regressions in Table 2, then back transformed. Because measurements for males and females were usually different (Fig. 2), midvalues between sexes were used. Percentage change is the change in a measurement between neighboring regions as a percentage of the measurement's range over the geographic range.

Inflections and Sexual Crossover in the Regressions

I examined 216 computer-drawn scattergrams for sexes within regions that represented the measurement regressions (Table 2), by transparent overlay with incised straight line. None shows obvious curvature, and only three show possible inflections: In females, the regression appears to bend upward about 8.3° at about 262 mm SL for belly measurements in the Atka-Bering region; downward about 7.0° at about 242 mm SL for hind-trunk ventral in the same region; and possibly upward about 13.5° at about 260 mm SL for the belly in the Southeastern region. Whether the apparent breaks in the three regressions are artifacts or real is moot. Evidence for reality includes their visibility in scattergrams; that all occur in a single sex (females) and in a measurement possibly influenced by sexual development with growth; and that the possible break in the belly regression in the Atka-Bering region has a near complement in the hind-trunk ventral measurements, which extend from the belly to the tail. Also, as discussed in a succeeding paragraph, mild inflections probably are hidden in variability of the data. Evidence against reality includes the extreme rarity of visible indications of possible breaks (none in 16 of 18 measurements and only 3 in the remaining 24 regressions), and the extreme goodness of fit (R^2) to a straight line shown by the regressions with possible inflections (Table 2). The measures for goodness of fit for belly are the best among regions in the two regressions with possible inflections, and both measures are higher than those for corresponding male regressions, which show no indications of inflection. The weight of evidence seems to side with the visible breaks being artifacts. Yet, even if the breaks represent real inflections, the morphometric data seem to fit linear criteria well as far as conventional measures are concerned.

The regressions for sexes, within measurements and regions (Table 2), diverge with increasing SL, indicating that sexual dimorphism increases with growth. The increases are slight, however, as evidenced by the similarity in regression parameters between sexes, and on average, characters will differ in size between sexes by only a few millimeters in the standard 260 mm SL fish (Fig. 2). Given normal variation, the differences should not be obvious or reliable in differentiating sexes by gross examination of even the largest Pacific ocean perch.

However, divergent sexual-regression pairs pose an apparent contradiction when they intersect within their data domain. Such intersections infer 1) sexual differences in fish on the juvenile side of the intersection, 2) differences on the juvenile side the reverse of those on the adult side, and 3) differences between sexes in juveniles that increase as SL's become smaller. In the morphometric data, the regressions for sexes do intersect, and the intersections form a symmetrical unimodal distribution with a strong peak near 230 mm SL. By itself, crossover need not be a problem; e.g., the symmetrical confidence limits about regression (Sokal and Rohlf 1969) are evidence that crossover within these limits is normal in samples from a single population. Yet, differences in measurements for sexes on the juvenile side of the modal point for sexual crossovers apparently are greater than can be accommodated by confidence limits based on the regressions. In 108 comparisons of mean estimates for measurements and their confidence limits at 170 mm SL, 18 have significant differences, when only about 5 are expected with 95% confidence limits. Apparently, sexually associated crossover is slightly too severe in the morphometric data to be adequately contained by confidence limits for single populations.

The evidence is strong that most of the measurement regressions do not fit their data perfectly and, because of the nature of the error, that slight growth inflections likely are concealed by variation. The three apparent inflections mentioned previously might indicate the size at inflection, but the evidence is weak. It is apparent, however, that significant sexual differences in measurements at SL's below the crossover mode should not be taken literally. (Assuming that measurement regressions may incorporate hidden inflections, most reliable estimates of juvenile measurements among sexual pairs within their data domains will be from the regression whose slope is nearest unity, particularly if the sample number is large and the slope not significantly different from unity.) Because the bulk of specimens were larger than 230 mm SL, and the regressions fit their data closely, conclusions regarding adult relationships in the present data, particularly trends, should be reliable.

Strength of Geographic and Sexual Variation Shown in the Characters

Analysis of morphological diversity is most use-

ful where assigned components of variation can be maximized relative to unassigned components. I compared indices of variation assignable to measurement size (standard specimens), geographic, and sexual causes in the 18 characters by means of the alternate standard deviation (see Methods). First, I investigated relationships between variation and the size of a character. When mean responses for measurements in standard-sized fish from the Kodiak region were used as a basis of comparison, variability was positively related to size of the character, with the two variates significantly correlated (Fig. 4).

Size accounted for about 62% (R^2) of the variation between characters. To remove its effect in further comparisons, I used an alternate version of the coefficient of variation; i.e., the alternate standard deviation for each character divided by a size index (Kodiak) for that character $\times 100$. Although the alternate coefficient of variation reduced the unassigned variability, some sizable differences remained between characters (Table 3)—major dimensions of the head and dorsum varied least, fin spines and small features of the head varied most, and the symphyseal knob varied considerably more than any other character. With the exception of belly, the major trunk

TABLE 3.—Evidence for unassigned variation in measurements in Pacific ocean perch after correction for measurement size. Measurements ($\hat{Y}$) are related to a standard-sized fish of 260 mm SL from the Kodiak region by regressions in Table 2. Relative variation for each measurement is indexed by the alternate coefficient of variation (ACV) (see text) pooled over all regions and expressed as a percentage. Measurements arranged by increasing alternate coefficient of variation in the last column.

	Males		Females		Both sexes	
Measurement	$\hat{Y}$, mm	ACV	$\hat{Y}$, mm	ACV	$\hat{Y}$, mm	ACV
Nape	88.66	2.50	88.36	2.29	88.52	2.40
Head	88.22	3.32	87.07	2.53	87.66	2.94
Pelvic insertion	103.03	3.20	101.42	3.01	102.24	3.11
Body-depth pelvic	78.75	3.53	78.27	3.04	78.52	3.29
Hind-trunk dorsal	95.62	3.01	95.46	3.72	95.54	3.36
Spinous dorsal-fin length	92.01	3.43	91.92	3.63	91.97	3.53
Body-depth anal	63.31	4.19	62.52	3.51	62.92	3.86
Caudal peduncle	21.43	4.08	21.06	3.65	21.25	3.87
Longest pectoral-fin ray	64.91	4.43	63.82	4.10	64.38	4.27
Hind-trunk ventral	91.22	4.98	89.07	4.69	90.07	4.84
Upper-jaw length	36.60	6.43	36.89	5.43	36.74	5.94
3d anal-fin spine	28.99	6.68	28.87	6.61	28.93	6.64
6th spinous ray in dorsal fin	30.36	7.92	29.78	7.58	30.08	7.76
Belly	75.97	8.82	79.66	7.87	77.77	8.36
Upper-jaw width	12.15	9.86	12.17	7.54	12.16	8.73
13th spinous ray in dorsal fin	22.11	9.45	21.81	10.05	21.96	9.74
Orbit	22.73	9.57	22.46	10.32	22.60	9.94
Symphyseal knob	5.05	13.51	5.04	14.59	5.04	14.04

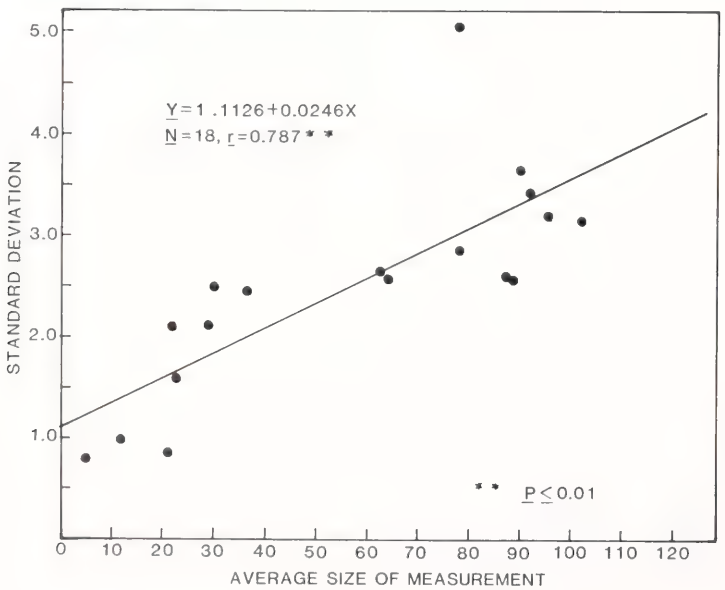

FIGURE 4.—Relationship between absolute size and variability of measurements in Pacific ocean perch. Character sizes are mean responses for hypothetical 260 mm SL fish from the Kodiak region as estimated from the regressions of Table 2; variability is estimated by alternate standard deviations for each character (see Methods) pooled over all regions.

dimensions had the lowest unassigned variability when corrected for size.

As would be expected from the plots of character measurements (Fig. 2), sexual and geographic variation were important components after the size effects were removed (Table 4). For sexual variation, the hind-trunk dorsal, spinous-dorsal fin, and body-depth pelvic measurements were the poorest discriminators, and belly, hind-trunk ventral, and longest pectoral-fin ray the best. For geographic variation, 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin were the poorest discriminators, and belly, hind-trunk ventral, and head measurements the best.

Present Nominal Subspecies are Questionable

Barsukov (1964) synonymized the nominal species *Sebastodes alutus* (Gilbert) and *S. paucispinosus* (Matsubara) but suggested that the eastern and western Pacific representatives may be separate subspecies: *S. a. paucispinosus* ranging from Honshu to Olyutorskii Bay and along the northern Bering Sea slope, perhaps to Bristol Bay; and *S. a. alutus* ranging from California to the Gulf of Alaska and along the Aleutian Arc to, and including, the Commander Islands. Barsukov morphologically distinguished the subspecies by "Alaskan *Seb. alutus* longer than 23 cm are quite noticeably distinguished from *Seb. alutus* from other parts of the range by body depth", and in a key gives the principal subspecies discriminator as whether the ratio SL/body depth of 170-360 mm SL fish is greater than 3.2 (*S. a. alutus*) or less (*S. a. paucispinosus*).

The question of eastern and western subspecies in *S. alutus* seems more complex than Barsukov (1964) suggested. The weight of present evidence, although preliminary, does not seem to justify the nominal subspecies. First, there is the problem of how populations sympatric over a distance as great as the Aleutian Arc could maintain reproductive isolation adequate to insure genetic distinctiveness. There is no evidence for isolating mechanisms in the species—on the contrary, the larvae are pelagic (Hart 1973), which should promote rapid genetic exchange over major distances

TABLE 4.—Relative degree that measurements in standard-sized Pacific ocean perch of 260 mm SL reveal geographic and sexual variation. In the variation sections, variation not related to character size was indexed by alternate coefficients of variation that were pooled over all samples, sexual variation was indexed by differences between sexes as a percentage of their mid-size in each region (positive if males averaged larger than females and negative if males were smaller, but only absolute values were used in calculations), and geographic variation was indexed by the maximum difference between regions as a percentage of mean-estimate size of measurements from the Kodiak region (Table 3). In the discrimination section, indices indicate relative magnitudes of sexual and geographic variation relative to variation not related to character size. Low values or ranks (in parentheses) indicate that variation not related to character size was high relative to sexual (data column 4) or geographic (data column 5) variation; hence, the measurement is a poor indicator of sexual or geographic variation, and vice versa. Kendall Coefficient of Concordance (Siegel 1956) between ranks for sexual and geographic variation was not significant.

Character	Variation not related to character size	Relative variation		Discrimination	
		Sexual	Geographic	(Sexual ÷ col. 1) × 10	Geographic ÷ column 1
Nape	2.91 (1)	0.493 (4)	4.60 (7)	1.69 (10)	1.58 (13)
Spinous dorsal-fin length	3.73 (6)	(−)0.088 (2)	4.39 (5)	0.24 (2)	1.18 (9)
Hind-trunk dorsal	3.35 (4)	(−)0.019 (1)	3.80 (2)	0.06 (1)	1.13 (7.5)
Hind-trunk ventral	4.05 (9)	2.038 (17)	9.57 (15)	5.03 (17)	2.36 (17)
Belly	6.45 (11)	(−)3.873 (18)	16.47 (18)	6.00 (18)	2.55 (18)
Pelvic insertion	3.08 (3)	0.875 (11)	6.53 (12)	2.84 (14)	2.12 (15)
Head	3.07 (2)	1.104 (13)	6.69 (13)	3.60 (15)	2.18 (16)
Body-depth pelvic	3.63 (5)	(−)0.104 (3)	4.32 (4)	0.29 (3)	1.19 (10)
Body-depth anal	4.21 (10)	0.628 (8)	6.19 (11)	1.49 (9)	1.47 (11)
Caudal peduncle	4.02 (7.5)	0.828 (9)	4.53 (6)	2.06 (13)	1.13 (7.5)
Orbit	7.01 (13)	0.503 (5)	13.39 (17)	0.72 (6)	1.91 (14)
Longest pectoral-fin ray	4.02 (7.5)	1.663 (16)	6.03 (10)	4.14 (16)	1.50 (12)
Upper-jaw length	6.68 (12)	1.305 (14)	4.93 (8)	1.95 (12)	0.74 (4)
Upper-jaw width	8.09 (15)	0.970 (12)	9.03 (14)	1.20 (8)	1.12 (6)
Symphyseal knob	15.49 (18)	0.873 (10)	11.29 (16)	0.56 (4)	0.73 (2.5)
6th spinous ray in dorsal fin	8.21 (16)	1.410 (15)	5.97 (9)	1.72 (11)	0.73 (2.5)
13th spinous ray in dorsal fin	9.54 (17)	0.589 (6)	0.94 (1)	0.62 (5)	0.99 (5)
3d anal-fin spine	7.31 (14)	0.602 (7)	3.87 (3)	0.82 (7)	0.53 (1)

and erase local differentiation. Further, the species appears to be genetically nearly homogeneous over as great, and environmentally variable, a distance in the eastern part of its range—Seeb and Gunderson (in press) demonstrated "very high similarity" among populations from Washington State to the Bering Sea and found no evidence for a barrier at the Aleutian Chain. Second, as already mentioned, morphological (including morphometric) differences can be environmentally induced through modification of growth rate. The growth differences Quast (fn. 2) found, which appeared to conform more closely to latitude than ocean temperatures, resemble geographic trends in some measurements examined in the present study, including body-depth pelvic (Fig. 2H). Last, Barsukov's criteria for the subspecies can be called into question. When referred to fish of two standard sizes, 260 and 300 mm SL, my data on body-depth pelvic (Barsukov's "body depth") indicate that only representatives from the Kodiak region have 95% confidence limits for *mean* population values that lie consistently on the *S. a. alutus* (the nominal eastern subspecies) side of Barsukov's criterion–confidence limits for most measurement means for other regions indicate ambiguous or improper identification (Table 5), and that a majority of specimens will be improperly identified. Further, neighboring populations in the eastern subspecies' range frequently differ significantly in one or more measurements (Fig. 2, Table 2). If significant geographic variation were a sole criterion for subspecies then a number might need be named.

Barsukov (1964) gave further criteria for separating the nominal eastern and western subspecies, but the criteria seem subjective and impractical: Prominence and apparent squamation of occipital crests do not seem of value; as I have observed, development of crests may be highly variable within regions, and evidence for squamation can be altered in specimens collected by bottom trawl. His analysis of variation in the occipital crests is too short and subjective to be useful. Size of symphyseal knob ("larger at similar body lengths in the eastern subspecies") is not reliable because the character has considerable

TABLE 5.—Mean, upper, and lower 95% confidence limits for the mean of body-depth pelvic (BDP) measurements and their derived proportions of standard length (SL) for Pacific ocean perch of 260 and 300 mm SL. Ratios of SL divided by body depth are categorized according to Barsukov's (1964) criterion of 3.2 for the ratio as follows: Ratios rounding to greater than the interval 3.15-3.24 (3.2 expanded to its inclusive values with two decimal points) are followed by a blank, those within the interval are followed by an "A", and those lower are followed by an "I". Ratios followed by a blank would identify the eastern nominal subspecies (*S. a. alutus*) by the 3.2 criterion, those followed by an "A" would give an ambiguous identification (*S. a. alutus* or *S. a. paucispinosus*), and those followed by an "I" would identify the western nominal subspecies (*S. a. paucispinosus*).

Region (limit)	260 mm SL				300 mm SL			
	Males		Females		Males		Females	
	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP	BDP	SL/BDP
Atka-Bering								
Lower	81.909	3.17 A	82.665	3.15 A	94.715	3.17 A	95.717	3.13 I
Mean	81.422	3.19 A	82.258	3.16 A	94.006	3.19 A	95.183	3.15 A
Upper	80.957	3.21 A	81.853	3.18 A	93.302	3.22 A	94.652	3.17 A
Atka-Gulf								
Lower	80.115	3.25	80.145	3.24 A	92.859	3.23 A	93.687	3.20 A
Mean	79.666	3.26	79.708	3.26	92.044	3.26	92.964	3.23 A
Upper	79.219	3.28	79.274	3.28	91.236	3.29	92.247	3.25
Kodiak								
Lower	79.214	3.28	78.662	3.31	91.513	3.28	91.554	3.28
Mean	78.753	3.30	78.269	3.32	90.928	3.30	90.870	3.30
Upper	78.295	3.32	77.878	3.34	90.346	3.32	90.389	3.32
Yakutat								
Lower	81.560	3.19 A	81.271	3.20 A	94.997	3.16 A	94.278	3.18 A
Mean	80.828	3.22 A	80.600	3.23 A	93.877	3.20 A	93.236	3.22 A
Upper	80.102	3.25	79.934	3.25	92.770	3.23 A	92.186	3.25
Southeastern								
Lower	81.125	3.20 A	81.878	3.18 A	94.906	3.16 A	95.531	3.14 I
Mean	80.655	3.22 A	81.239	3.20 A	94.224	3.18 A	94.540	3.17 A
Upper	80.187	3.24 A	80.605	3.23 A	93.547	3.21 A	93.559	3.21 A
Vancouver								
Lower	83.391	3.12 I	82.356	3.16 A	97.376	3.08 I	97.027	3.09 I
Mean	82.304	3.16 A	80.629	3.22 A	96.616	3.11 I	95.938	3.13 I
Upper	81.231	3.20 A	78.958	3.29	95.861	3.13 I	94.861	3.16 A

unassigned variation for its size (Table 3), as well as high positive allometry (Table 2).

The possibility exists, since Barsukov (1964) measured body depth directly on preserved specimens, a method different from that used in the present paper, that the two methods give biased measurements relative to the other. The question cannot be fully resolved; Barsukov gave sparse collection information (e.g., his conclusions on Bristol Bay representatives were based on eight or fewer specimens between 30 and 340 mm SL), and he gave no data on statistical parameters or data peculiarities. Although the body depth measurement at pelvic fins is simple to perform, high accuracy and undistorted material are necessary because geographic variation is slight but significant (e.g., maximum geographic difference between means for body-depth pelvic at 260 mm SL is around 4 mm in Figure 2H).

Indirect evidence indicates that the combination of photogrammetry and fresh specimens used in the present study probably gave more precise measurements than the hand methods and museum specimens used by Barsukov (1964), but likely that bias between methods was unimportant relative to other factors. Barsukov stated that body depth in specimens attributed by him to *S. a. paucispinosus,* presumably including those from Bristol Bay, averages 3.05 into SL, and that his specimens of *S. a. alutus* average 3.42. In contrast, in the present study, the extreme regional confidence limits for means lie between 3.08 and 3.34 (Table 5), well within the span of Barsukov's means (my data for Bristol Bay are nearly central between his values, with confidence limits of 3.12 and 3.22).

Rather than methods bias, the wide range of mean values for body depth given by Barsukov (1964) relative to those in Table 5 may have been caused in part by chance overweighting of extreme data values because of his relatively small sample sizes. His 124 specimens were relatively few for a considerable geographic range—82 from Bristol Bay to Washington and 42 from Olyutorskii Bay and the Commander Islands. Perhaps, body-depth variation was falsely indicated as bimodal in Aleutian Arc representatives, leading to the interpretation that the data represented shallow- and deep-bodied populations.

Finally, Barsukov may have been misled by variable distortion and shrinkage of his specimens owing to conditions of preservation and storage. Although he stated that his specimens shortened 0.3-4.0% after "several" months of preservation in alcohol, and that 200 mm SL fish lost 1% and 300 mm fish lost 2% on average, he apparently did not try to compensate for this loss in length and apparently did not measure corresponding changes in body depth at the pelvic fins. Some of his material had been preserved much longer than several months and may have been even less representative of fresh material—the Olyutorskii Bay and Commander Island specimens were collected by A. P. Andriyashev in 1932 and 1950-52, indicating probable 9-30 yr storage in alcohol before measurement.

CONCLUSIONS

Because geographic variation was expressed in all parts of the morphology of Pacific ocean perch that I investigated, I conclude that the variation pervades body growth in the species. Over the eastern Bering Sea and eastern Pacific Ocean, adult measurements usually vary as V-shaped clines. Here, representatives of the same SL from the extremes of the sampling range (Vancouver Island and the eastern Bering Sea) resemble each other more than they resemble fish from near the midrange (Kodiak and Yakutat regions), where measurements often are smallest.

Only measurements of belly size and neighboring parts of the body have single, monotonic clines over the regions. Belly size increases dramatically from Vancouver Island to the eastern Bering Sea accompanied by corresponding size decreases in neighboring body measurements. The anterior and posterior boundaries of the belly, pelvic girdle (given by pelvic insertion), and anal-fin spines (given by body-depth anal) move relationally farther apart to give progressively larger bellies in populations farther from Vancouver Island and closer to the Bering Sea. Length of the spinous dorsal fin generally increases from southeast to northwest and length of the nape decreases, both apparently because of a relationally forward shift in the anterior insertion of the dorsal fin.

Nearly all morphometric characters apparently grow allometrically in Pacific ocean perch, but average body form does not change markedly with growth because allometric coefficients of most characters are near unity. Often, measurements vary between apparent slight but significant positive and negative allometry, depending on the sampling region. The symphyseal knob and 3d anal-fin spine (allometric coefficients were 1.52 and 0.73, respectively, including both sexes)

may be sufficiently allometric for the symphyseal knob to seem exceptionally prominent and the 3d anal-fin spine exceptionally small in some large specimens.

Most body dimensions average smaller in females than in males, but bellies are larger in females. The same mechanism, opposing relational movements of the pelvic girdle and the anal-fin spines, is responsible for sexual and geographic variation in belly size. Although sexual dimorphism increases with growth, sexual differences are not prominent and have broadly overlapping distributions. As a result, sexes probably cannot be reliably identified by gross examination of any of the 18 characters.

Neither geographic nor sexual variation is quantitatively similar between measurements in Pacific ocean perch—characters tend to vary with their absolute size. Overall, geographic variation is most poorly discriminated by the measurements of the 3d anal-fin spine, symphyseal knob, and 6th spinous ray in dorsal fin, and best discriminated by the belly, hind-trunk ventral, and head. Sexual dimorphism is most poorly discriminated by the measurements of the hind-trunk dorsal, spinous dorsal-fin length, and body-depth pelvic, and best discriminated by the belly, hind-trunk ventral, and pelvic insertion. Measurements that have been used for taxonomy of Pacific ocean perch in the past are relatively poor discriminators of geographic variation or possible genetic stocks or subspecies. Although body form changes significantly with geographic region, sex, and growth, differences are too small and unexplained variation too large for differences to be of value for distinguishing single specimens geographically.

Because of questions concerning validity and importance of published morphological information supporting supposed subspecies of Pacific ocean perch, it seems prudent that further claims for subspecies based on morphology be postponed until variation is reliably assessed over the entire species' range and definitive characteristics are known to be genetically based.

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GENETIC VARIATION IN CHINOOK, *ONCORHYNCHUS TSHAWYTSCHA*, AND COHO, *O. KISUTCH*, SALMON FROM THE NORTH COAST OF WASHINGTON

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ABSTRACT

We used starch-gel electrophoresis to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, in the major drainages of the north coast of Washington (the Quillayute, Hoh, Queets, and Quinault Rivers). Of 55 loci examined for electrophoretically detectable variation, 6 were polymorphic (frequency of the common allele was less than 0.95) in chinook salmon and 3 in coho salmon. Statistical tests of interdrainage and intradrainage variation for coho salmon were tenuous because most of the fish examined were from a single year class so that we could not account for variation among year classes. Nevertheless, these tests suggested that distinct stocks of coho salmon exist within drainages, and that variation was not significantly greater among drainages than within drainages. Interdrainage variation for wild chinook salmon was not significant. The data suggested that summer chinook salmon were electrophoretically different from fall chinook salmon, and the hatchery populations of chinook salmon were distinct from wild fish. A hatchery population developed primarily from north coast fish was electrophoretically more similar to wild chinook salmon than were the others.

Effective conservation and management of natural organisms require protection of the genetic resources (genes, gene combinations, gene pools) of these organisms (Altukhov 1981; Frankel 1983). Conservation of anadromous salmonids from the north coast of Washington (the area from the Quinault River to the Strait of Juan de Fuca) is receiving national attention because many of these fish spawn or rear in Olympic National Park, and the United States Congress has directed that the natural resources of National Parks be conserved. Olympic National Park is the only natural area administered by the National Park Service outside Alaska with substantial numbers of native anadromous salmonids. There is also international concern for conservation of natural (including genetic) resources in Olympic National Park, as indicated by inclusion of the park in the International Biosphere Reserve Program (Franklin 1977).

The present study was initiated to genetically characterize the populations of chinook salmon, *Oncorhynchus tshawytscha*, and coho salmon, *O. kisutch*, from the major drainages of the north coast: the Quillayute, Hoh, Queets, and Quinault Rivers (Fig. 1). Coho salmon from two other streams in northwestern Washington (the Snohomish River and Snow Creek) and chinook salmon from Elwha Hatchery and the Wynoochee River were also sampled to enhance our perspective for examining north coast fish. Chinook and coho salmon are native to the west coast of North America from California to Alaska (Scott and Crossman 1973) and are the only species of Pacific salmon that are abundant in each of the major north coast drainages. Starch-gel electrophoresis was used to genetically characterize the fish.

Our objectives were 1) to develop a baseline set of allele frequency data; 2) to determine whether allele frequencies varied among major drainages; 3) to determine the degree of genetic structuring in coho salmon within major drainages; 4) to determine whether summer chinook salmon are electrophoretically distinct from fall chinook salmon; and 5) to determine whether hatchery populations of chinook salmon are electrophoretically distinct from wild (i.e., naturally spawned) fish.

We could not examine genetic structuring in chinook salmon within major drainages because wild adults were sampled in the lower portions of the rivers and thus their destinations within the major drainages were unknown, and samples of

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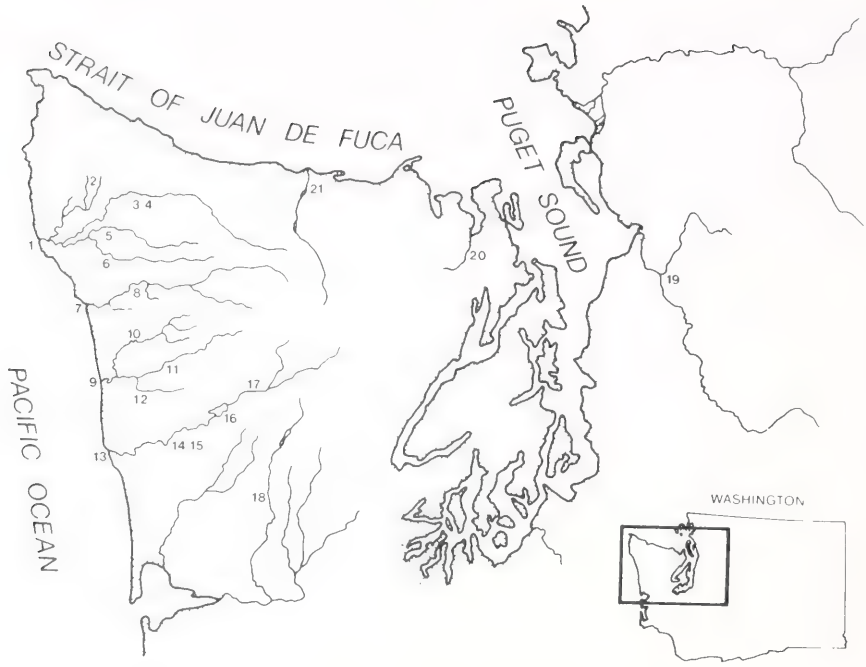


FIGURE 1.—Study area in northwestern Washington. This study focused on the four major stream systems of the north coast: the Quillayute (1), Hoh (7), Queets (9), and Quinault (13) drainages. Numbers identify sampling areas ("nets" indicates that adults were taken in the Indian gill net fisheries): (1) Quillayute River (nets); (2) Dickey River; (3) Soleduck River; (4) Soleduck Hatchery; (5) Calawah River; (6) Bogachiel River; (7) Hoh River (nets); (8) Hoh River; (9) Queets River (nets); (10) Clearwater River; (11) Upper Queets River, i.e., above the Salmon River; (12) Salmon River; (13) Quinault River (nets); (14) Lower Quinault River, i.e., below Lake Quinault; (15) Quinault National Fish Hatchery; (16) Quinault pens; (17) Upper Quinault River, i.e., above Lake Quinault; (18) Wynoochee River; (19) Snohomish River; (20) Snow Creek; (21) Elwha Hatchery.

wild juveniles contained unknown proportions of fish from genetically distinct runs.

MATERIALS AND METHODS

Three "runs" of chinook salmon and two runs of coho salmon occur in the study area. The runs are primarily distinguished by the time of year when the fish return to fresh water as adults. In general, spring chinook salmon return to fresh water from March to early June, summer chinook salmon from late June to August, and fall chinook salmon from mid-September to November. Similarly, summer coho salmon return to fresh water during August and early September, and fall coho salmon return from mid-October through November. Spring chinook salmon and summer coho salmon were not included in this study because returns to fresh water were low and few of these fish were available during our study. Adult salmon spawn in the autumn, and juveniles emerge from the gravel during the following winter or spring. Juvenile chinook salmon typically remain in the streams for several weeks to several months after emerging from the gravel, and enter the ocean during the summer or autumn; juvenile coho salmon remain in the streams for a year and enter the ocean during the spring.

Almost all summer coho salmon in the study area spawn in the Soleduck River (Quillayute River system) above Salmon Cascades (Houston 1983[3]). Our samples of fall-run juvenile coho salmon for the Soleduck River were taken from tributaries below Salmon Cascades to reduce the chance of including summer-run fish.

In addition to the fish rearing in streams,

[3]Houston, D. B. 1983. Andromous fish in Olympic National Park: a status report. Unpubl. rep. U.S. National Park Service, Port Angeles, WA.

salmon are raised in one federal, one state, and two tribal hatcheries along the north coast. Samples were taken from six hatchery populations (Table 1).

Table 1.—Run times and stock origins for hatchery populations used in genetic characterization.

Species of salmon	Run	Hatchery	Stock origin[1]
Chinook	Fall	Quinault National Fish Hatchery (Quinault NFH)	Quinault River and transfers from Hoh and Queets Rivers, and University of Washington, Willapa, Nemah, Finch Creek, Deschutes, Green River, and Samish Hatcheries.
Chinook	Fall	Quinault Tribal Penned Rearing Facility (Quinault Pens)	Queets River and transfers from Quinault, Green River, Samish, and Deschutes Hatcheries.
Chinook	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.
Chinook	Spring-summer	Washington Department of Fisheries Soleduck Hatchery	Soleduck River and transfers from Dungeness, Cowlitz, and Umpqua Hatcheries.
Coho	Fall	Quinault NFH	Transfers from Quilcene, Purdy Creek, Moclips, Willapa, Soleduck, Simpson, Skagit, Green River, Hood Canal, and Cowlitz Hatcheries.
Coho	Fall	Washington Department of Fisheries Soleduck Hatchery	Primarily Soleduck River; some transfers from Dungeness Hatchery.

[1]From Houston (see text footnote 3).

Sample Collection

Fish were collected during 1983 from the 21 areas identified in Figure 1 (some juvenile chinook salmon were also available from collections made in 1982). Juvenile fish at hatcheries were collected with dip nets at several locations along each raceway containing the fish to be studied. Juveniles in streams were collected by trapping, electrofishing, and seining. A few juvenile coho salmon (usually <15 in each age group) were taken from each of several sites throughout each drainage. Juvenile chinook salmon were taken from several sites in the lower portions of the rivers. Juveniles of both species were collected from areas where no hatchery fish were released or before hatchery fish were released; they were either kept alive or held on ice for up to 8 hours and then frozen at −10°C or −70°C until thawed for electrophoretic analysis.

Samples of tissue from eye, liver, white muscle, and heart were taken from adult fish spawned at hatcheries or caught in gill net fisheries at the mouths of the rivers. At the hatcheries, samples of tissue were taken within 3 hours after the fish were killed for spawning. Adults from the fisheries were not available to us until they had been delivered to wholesale fish buyers. Some fish were delivered more than a day after the fish were killed; although most were kept on ice or refrigerated during this interval, some isozyme activity was lost. Tissue samples from all adults were placed on ice within 30 minutes after excision and were frozen at −10°C or −70°C within 6 h.

Electrophoresis

We used horizontal starch-gel electrophoresis (Utter et al. 1974; May et. al. 1979) to assay fish tissues. Eye, heart, liver, and muscle tissues were removed from partly thawed juveniles just before electrophoretic analysis. We identified alleles at loci encoding specific enzymes, using the staining methods of Harris and Hopkinson (1976) and Allendorf et al. (1977). The nomenclature used to describe the gene loci and the allele variants followed Allendorf and Utter (1979).

Of the 40 enzymes examined, 30 had sufficient activity and resolution to be used in this study

(Table 2). Initially all 30 enzymes were examined in all fish; in later samples, however, we omitted the loci in chinook salmon that had been determined to be monomorphic in previous studies or in our initial screening.

TABLE 2.—Enzymes and loci examined in chinook and coho salmon. Enzyme commission numbers are in parentheses. Tissue E refers to eye, H to heart, L to liver, and M to white muscle. Buffer system 1 was described by Ridgway et al. (1970), 2 by Clayton and Tretiak (1972), and 3 by Markert and Faulhaber (1965) and Kobayashi et al. (1984).

Enzyme	Chinook salmon			Coho salmon		
	Loci	Tissue	Buffer	Loci	Tissue	Buffer
β-N-Acetyl-galactosaminidase (3.2.1.23)	[1]*bGala-2*	L	2	[1]*bGala-1*	L	2
				bGala-2	L	2
N-Acetyl-B-glucosaminidase (3.2.1.30)	[1]*bGa-1*	L	1	[1]*bGa-1*	L	1
Acid phosphatase (3.1.3.2)	[1]*Acp-1*	L	2	[1]*Acp-1*	L	2
	[1]*Acp-2*	L	2	[1]*Acp-2*	L	2
Aconitate hydratase (4.2.1.3)	[1]*Ah-1*	H	2	[1]*Ah-1*	H	2
	[1]*Ah-2*	H	2	[1]*Ah-2*	H	2
	Ah-3	L	2	*Ah-3*	L	2
Adenosine deaminase (3.5.4.4)	—	—	—	[1]*Ada-1*	M	1,3
				Ada-2	M,E	1,3
Adenylate kinase (2.7.4.3)	[1]*Ak-1*	M	2	[1]*Ak-1*	M	2
Alanine aminotransferase (2.6.1.2)	[1]*Alat-1*	M	1	[1]*Alat-2*	M	1
Alcohol dehydrogenase (1.1.1.1)	*Adh-1*	L	2	[1]*Adh-1*	L	2
Aspartate aminotransferase (2.6.1.1)	[1]*Aat-1*	L	2	[1]*Aat-1,2*	L	2
	[1]*Aat-3,4*	M	2	*Aat-3,4*	M	2
	[1]*Aat-5*	E	2	[1]*Aat-5*	E	2
Creatine kinase (2.7.3.2)	[1]*Ck-1*	M	1	*Ck-1*	M	1
	[1]*Ck-2*	M	1	[1]*Ck-2*	M	1
	[1]*Ck-3*	M	1	[1]*Ck-3*	M	1
Diaphorase-NADH (1.6.*.*)	[1]*Dia-1*	L	1	[1]*Dia-1*	L	1
Diaphorase-NADPH (1.6.*.*)	[1]*DiaP-1*	L	1	[1]*DiaP-1*	L	1
Fructose bisphosphate aldolase (4.1.2.3)	[1]*Fbald-1*	E	2	[1]*Fbald-1*	E	2
	[1]*Fbald-2*	E	2	[1]*Fbald-2*	E	2
Fumarate hydratase (4.2.1.2)	[1]Fh-1	M	1	[1]*Fh-1*	M	1
Glucose-6-phosphate isomerase (5.3.1.9)	[1]*Gpi-1*	M	1	*Gpi-1*	M	1
	Gpi-2	M	1	*Gpi-2*	M	1
	Gpi-3	M	1	*Gpi-3*	M	1
β-Glucuronidase (3.2.1.31)	[1]*bGus-1*	L	1	[1]*bGus-1*	L	1
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	[1]*Gapdh-3*	E	2	[1]*Gapdh-3*	E	2
	[1]*Gapdh-4*	E	2	[1]*Gapdh-4*	E	2
Glycerol-3-phosphate dehydrogenase (1.1.1.8)	[1]*G3pdh-1*	M	2	*G3pdh-1*	M	2
	[1]*G3pdh-2*	M	2	[1]*G3pdh-2*	M	2
	[1]*G3pdh-3,4*	H	2			
L-Iditol dehydrogenase (1.1.1.14)	*Iddh-1,2*	L	1	—	—	—
Isocitrate dehydrogenase (1.1.1.42)	[1]*Idh-1*	M	2	[1]*Idh-1*	M,H	2
	Idh-2	M	2	[1]*Idh-2*	M,H	2
	Idh-3,4	M,L	2	*Idh-3,4*	L,H	2
L-Lactate dehydrogenase (1.1.1.27)	[1]*Ldh-1*	M	1	[1]*Ldh-1*	M	1
	[1]*Ldh-2*	M	1	[1]*Ldh-2*	M	1
	[1]*Ldh-3*	E	1	*Ldh-3*	E	1
	[1]*Ldh-4*	L	1	*Ldh-4*	L	1
	[1]*Ldh-5*	E	1	[1]*Ldh-5*	E	1
Lactoylglutathione lyase (4.4.1.5)	[1]*Lgl-1*	E,M	1	*Lgl-1*	E,M	1
Malate dehydrogenase (1.1.1.37)	*Mdh-1,2*	L	2	*Mdh-1,2*	L	2
	Mdh-3,4	M	2	*Mdh-3,4*	M	2
Malate dehydrogenase (NADP+) (1.1.1.40)	[1]*MdhP-1*	M	2	*MdhP-1*	M	2
	[1]*MdhP-2*	M	2	[1]*MdhP-2*	M	2
	[1]*MdhP-3*	L	2	[1]*MdhP-3*	L	2
Mannose-6-phosphate isomerase (5.3.1.8)	*Mpi-1*	E	2	*Mpi-1*	E	2
α-Mannosidase (3.2.1.24)	[1]*aMan-1*	L	1	[1]*aMan-1*	L	1
Phosphoglucomutase (5.4.2.2)	*Pgm-1*	M	1	[1]*Pgm-1*	M	2
				Pgm-2	M	2
Phosphogluconate dehydrogenase (1.1.1.44)	*Pgdh-1*	M	2	*Pgdh-1*	M	2
Phosphoglycerate kinase (2.7.2.3)	[1]*Pgk-1*	M	2	[1]*Pgk-1*	M	2
	Pgk-2	M	2	[1]*Pgk-2*	M	2
Superdioxide dismutase (1.15.1.1)	*Sod-1*	L,H	1	[1]*Sod-1*	L	1,2
	[1]*Sod-2*	L	2			

[1]No isozyme variation observed.

Data Analysis

Goodness-of-Fit Tests

We used the chi-square test to examine genotype frequencies for deviation from the (Hardy-Weinberg) proportions expected with random mating. Cells with an expected number <5 were combined with the next larger cell. The significance level for each test was modified to account for the increase in type I error when multiple tests of the same hypothesis are made (Cooper 1968). Tests were considered significant if the chi-square statistic exceeded the critical value for chi-square associated with a probability of $0.05/n$, where n was the number of loci tested within a sample. In this way the overall probability of rejecting H_0 by chance alone was approximately $1 - (1 - 0.05/n)^n \cong 0.05$ for each sample. Genotypes for *Idh-3,4*, *Mdh-1,2*, and *Mdh-3,4* were not tested because these systems consisted of pairs of loci with identical electrophoretic mobility, and genotypes at each locus could not be determined.

The likelihood ratio test (G-test; Sokal and Rohlf 1981) was used to test equality in allele frequencies between year classes. Here also, cells with an expected number <5 were combined with the next largest cell. The G-statistics, summed over all loci, were considered significant if they exceeded the critical value for chi-square associated with a probability of $0.05/s$, where s was the number of samples tested. Samples from streams and samples from hatcheries were tested as separate groups. The correction for multiple comparisons was made because each of the three H_0—no interbrood variation by drainage, by streams within drainages, or by hatchery—was independently tested for several drainages, streams, or hatcheries, respectively.

Analysis of Variance

We used analysis of variance (ANOVA) to test interdrainage differences, differences between hatchery and wild chinook salmon, and differences between summer and fall runs of chinook salmon. Data for coho salmon were not tested by ANOVA because data were available for only one year class from most locations, and estimates of interbrood variation in allele frequencies would have come from only two sample locations. The data used were from the loci scored for fish from each major north coast drainage and with frequencies <0.95 for the common (100) allele. The values used in the analysis were the arcsin of the square root of the frequency of the common allele at each locus. Differences were tested by contrasts (Table 3) or by partitioning the sum of squares within a one-way ANOVA for each locus (Snedecor and Cochran 1967; SPSS, Inc. 1983). Groups included in this analysis were as follows (adults would have spawned in 1983):

Cell	*Group*	*Run*	*Replicate*
1	Quillayute River	Mixed	1981 brood
			1982 brood
2	Hoh River	Mixed	1981 brood
			1982 brood
3	Queets River	Mixed	1981 brood
			1982 brood
4	Quinault River	Mixed	1981 brood
			1982 brood
5	Wynoochee River	Mixed	1982 brood
6	Quinault Pens	Fall	1982 brood
7	Quinault NFH	Fall	1981 brood
			1982 brood
8	Soleduck Hatchery	Fall	1981 brood
			1982 brood
9	Hoh River	Fall	Adults
10	Queets River	Fall	Adults
11	Soleduck Hatchery	Spring-summer	(data from Milner et al. 1983[1])
			1982 brood
			Adults
12	Hoh River	Summer	Adults
13	Queets River	Summer	Adults

[1]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. Rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

Juveniles from the different runs of chinook salmon were morphologically indistinguishable and our estimates of error variance were probably inflated because they were based on samples (of juveniles) that vary from year to year in the proportion of fish from each race. As a result, the (discriminatory) power for detecting differences between groups was impaired. In view of this reduced discriminatory power, differences with $0.05 \leq P < 0.1$ were noted in the text; statistical significance, however, was reserved for differences with $P < 0.05$.

Adult fall and summer chinook salmon from the Quillayute River and adult fall chinook salmon from the Quinault River were not included in the ANOVA because adults returning to these streams include large numbers of hatchery fish (Houston fn. 3). Adult summer chinook

TABLE 3.—Chinook salmon—coefficients for contrasts (Snedecor and Cochran 1967) within the analysis of variance. Cell numbers refer to groups identified in text. Within each contrast, the mean allele frequencies for groups with positive coefficients were compared with the mean frequencies for groups with negative coefficients.

	Cell												
Contrast	1	2	3	4	5	6	7	8	9	10	11	12	13
Interdrainage variation													
1 Fall-run adults	0	0	0	0	0	0	0	0	−1	1	0	0	0
2 Summer-run adults	0	0	0	0	0	0	0	0	0	0	0	−1	1
Hatchery vs. wild													
3 Summer run	0	0	0	0	0	0	0	0	0	0	−2	1	1
Fall run:													
4 Quinault Pens	0	0	0	0	0	−2	0	0	1	1	0	0	0
5 Quinault NFH	0	0	0	0	0	0	2	0	1	1	0	0	0
6 Soleduck Hatchery	0	0	0	0	0	0	0	−2	1	1	0	0	0
Summer vs. fall													
7 Adults	0	0	0	0	0	0	0	0	−1	−1	0	1	1

salmon from the Quinault River were not included because many hatchery fall chinook salmon return to the Quinault River with the summer-run salmon (during August, when most of our sampling was done) and our samples probably included a high proportion of fall-run hatchery fish (Larry Gilbertson[4]).

Gene Diversity Analysis

We used a modification of Chakraborty's (1980) gene diversity analysis to examine the hierarchical structure of genic diversity among the samples of wild coho salmon from the north coast. This analysis partitions total gene diversity (H_t, heterozygosity of allele frequencies over locations) into interdrainage and intradrainage components (Nei 1973). We considered three levels of population subdivision (Fig. 2)—broods (b), streams within drainages (w), and drainages (d)—so that $H_t = H_s + D_{bw} + D_{wd} + D_{dt}$, where H_s is the average heterozygosity within samples, D_{bw} is the gene diversity between broods, D_{wd} is the diversity within drainages, and D_{dt} is the diversity among drainages. Relative gene diversities (G_{ij}) are the proportions of H_t associated with a particular hierarchical level; for example, $G_{wd} = D_{wd}/H_t$.

[4] Larry Gilbertson, Quinault Tribal biologist, Quinault Indian Nation, P.O. Box 189, Taholah, WA 98587, pers. commun. August 1983.

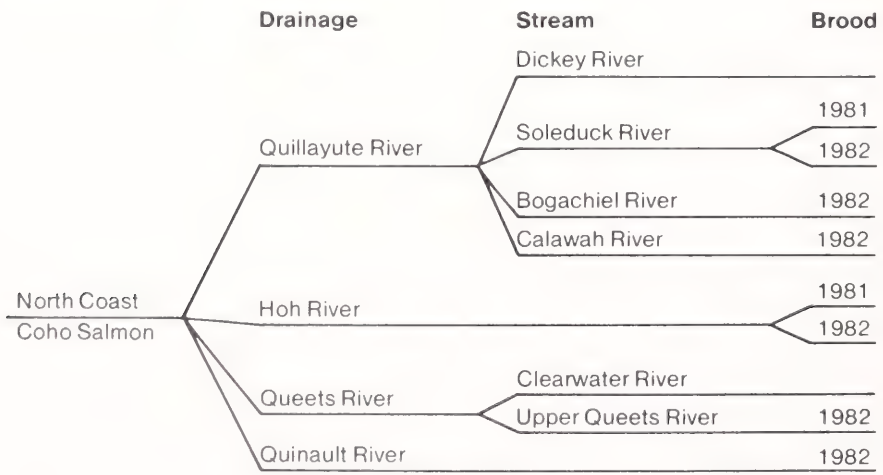


FIGURE 2.—Coho salmon—hierarchical subdivisions used in the gene diversity analysis for wild fish from the north coast of Washington (see test). Where brood is not identified, fish were from both the 1981 and 1982 broods.

The modification to Chakraborty's (1980) analysis consisted of giving equal weight to subgroups within a cell, rather than weighting them according to the number of samples within each subgroup. Our sampling design did not include all possible or desirable subgroups; the design was a compromise that allowed us to evaluate the different levels of subdivision and still remain within our budget. We felt that equal weighting was necessary because the number of subgroups within a cell usually did not reflect the "true" number of subgroups that may have existed for that cell. Donald Campton (University of Florida, Gainesville) provided a computer program, coded in Fortran 77, that included the required modification to Chakraborty's equations.

Cluster Analysis

The unweighted pair group method of cluster analysis (UPGM analysis; Sneath and Sokal 1973) and (nonmetric) multidimensional scaling (Gordon 1981; Kruskal and Wish 1977) were used to illustrate genetic similarities among samples. These two cluster analyses were applied to values of Nei's (1972) genetic distance calculated for each pair of samples. Data from the separate broods were pooled with equal weight for these analyses.

RESULTS

Chinook Salmon

Although fish from two locations showed significant deviation from Hardy-Weinberg proportions ($P < 0.05/n_i$ where n_i was the number of loci tested for location i)—juveniles of the 1982 brood from the Bogachiel River were deficient in heterozygotes at the *Pgk-2* locus and juveniles of the 1982 brood from the Hoh River had an excess of heterozygotes at the *Gpi-2* locus—these deviations are probably spurious, given the large number (20) of samples tested.

Interbrood variation in allele frequencies was significant ($P < 0.01$) for wild fish and for hatchery fish (Table 4). Six loci, or pairs of loci, showed sufficient variation and were scored for enough fish ($n > 25$) to be used in the ANOVA (Fig. 3, App. Table 1). Variation between drainages was not significant, although summer-run fish may differ between drainages ($P = 0.07$, Table 4). Hatchery fish were different from wild fish (contrasts 3 to 6 in Table 5).

The UPGM cluster analysis showed that the hatchery populations were distinct from wild juveniles and from all but one (Quinault River) sample of adults (Fig. 4). Of the hatchery populations, fall-run fish from Soleduck Hatchery were

TABLE 4.—Chinook salmon—likelihood ratio analysis of interbrood variation at 10 codominant loci. Significant levels were evaluated for totals only. *G* = likelihood ratio statistic.

	Ah-3		*Gpi-2*		*Idh-3,4*		*Mdh-3,4*		*Mpi-1*		*Pgm-1*		*Pgk-2*		*Sod-1*		Total	
	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*
Interbrood variation for drainages																		
Quillayute River	1	1.36	—	—	1	15.61	1	6.26	1	0.25	1	0.00	1	3.90	1	3.63	7	31.01**
Hoh River	2	2.66	—	—	1	10.21	—	—	1	1.78	1	3.22	1	0.09	1	0.21	7	18.16*
Queets River	1	0.00	—	—	1	0.05	—	—	1	2.73	1	0.19	1	1.12	1	0.32	6	4.41
Group total																	20	53.58†
Interbrood variation for streams (within drainages)																		
Soleduck River	1	4.77	—	—	—	—	—	—	1	1.83	1	0.65	1	4.79	1	3.85	5	15.89*
Bogachiel River	1	0.20	—	—	—	—	1	5.81	1	0.33	1	0.44	1	0.55	1	0.81	6	8.14
Hoh River	2	2.66	—	—	1	10.20	—	—	1	1.78	1	3.22	1	0.08	1	0.21	7	18.16*
Queets River above Salmon River	1	0.42	—	—	1	2.58	—	—	1	3.64	1	16.55	1	2.22	1	0.34	6	25.76**
Clearwater River	1	0.43	—	—	1	2.73	—	—	1	0.57	1	6.57	1	0.07	1	0.02	6	10.39
Group total																	30	78.34†
Interbrood variation for hatcheries																		
Soleduck Hatchery																		
Spring/summer	2	1.98	1	0.29	2	6.46	—	—	2	9.56	—	—	2	4.45	2	12.58	11	35.31**
Fall	1	2.26	—	—	—	—	—	—	1	0.89	—	—	—	—	1	0.31	3	3.46
Quinault NFH (Fall)	1	1.63	—	—	1	5.99	—	—	1	9.53	1	2.21	1	11.41	1	1.29	6	32.06**
Elwha Hatchery	—	—	1	9.58	—	—	—	—	1	2.28	—	—	1	7.15	1	0.30	4	19.34**
Group total																	24	90.17†

*$P < 0.05$ n | where $n = 3$ for interbrood variation within drainages, $n = 5$ for variation within streams, and $n = 4$ for variation within hatch-
**$P < 0.01$ n | eries. These are corrections for multiple comparisons (Cooper 1968).
†$P < 0.01$.

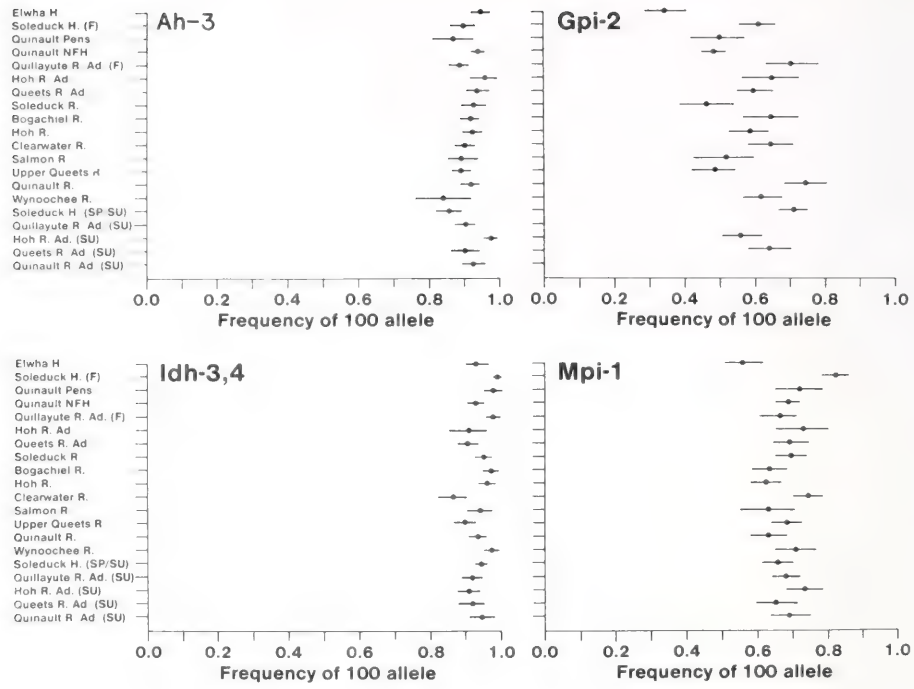


FIGURE 3a.—Chinook salmon—common-allele frequencies (q) for four protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

TABLE 5.—Chinook salmon—results from multivariate (MANOVA) and univariate analyses of the variance among frequencies (q) of the 100 allele at each of six loci or pairs of loci. Actual values in the analyses were transformed frequencies: arcsin $\sqrt{q}$. Hypothesis numbers correspond to those in the text table for contrasts under Materials and Methods. F = F statistics, df = degrees of freedom for the F statistics.

Hypothesis	*P* value from MANOVA		Tests at individual loci					
			Ah-3	*Idh-3,4*	*Mpi-1*	*Pgm-1*	*Pgk-2*	*Sod-1*
Interdrainage variation								
1 Fall run adults	0.54	F	0.15	0.00	0.14	0.52	0.27	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
2 Summer run adults	0.07	F	5.39	0.00	0.51	0.00	1.00	0.14
		df	1,7	1,7	1,7	1,7	1,7	1,7
Juveniles	—	F	0.43	1.45	0.54	0.38	0.85	0.31
		df	3,6	3,7	3,7	3,7	3,7	3,6
Hatchery vs. wild								
3 Summer run	0.34	F	11.46	0.54	0.44	22.15*	0.28	5.67
		df	1,7	1,7	1,7	1,7	1,7	1,7
Fall run								
4 Quinault Pens	0.03*	F	4.93	1.50	0.00	0.06	4.40	0.18
		df	1,7	1,7	1,7	1,7	1,7	1,7
5 Quinault NFH	0.06	F	0.18	0.33	0.09	0.53	8.91	7.45
		df	1,7	1,7	1,7	1,7	1,7	1,7
6 Soleduck Hatchery	0.03*	F	6.06	4.37	2.79	11.44	0.00	2.84
		df	1,7	1,7	1,7	1,7	1,7	1,7
Summer vs. fall								
7 Adults	0.06	F	0.00	0.05	0.10	1.32	1.71	0.67
		df	1,7	1,7	1,7	1,7	1,7	1,7

*$P < 0.05$ for MANOVA, or $P < 0.05/6$ for univariate tests.

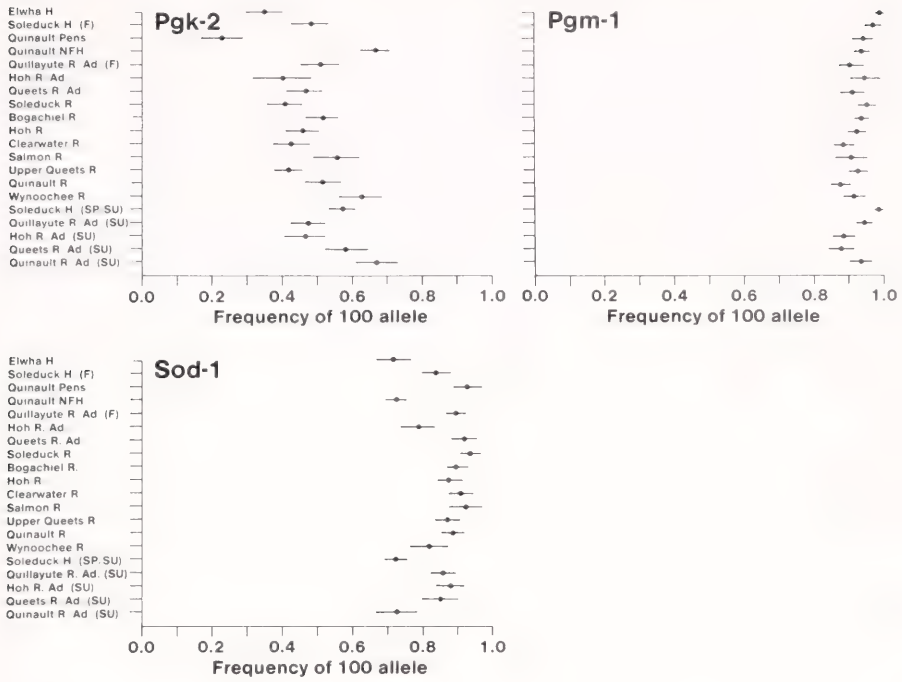
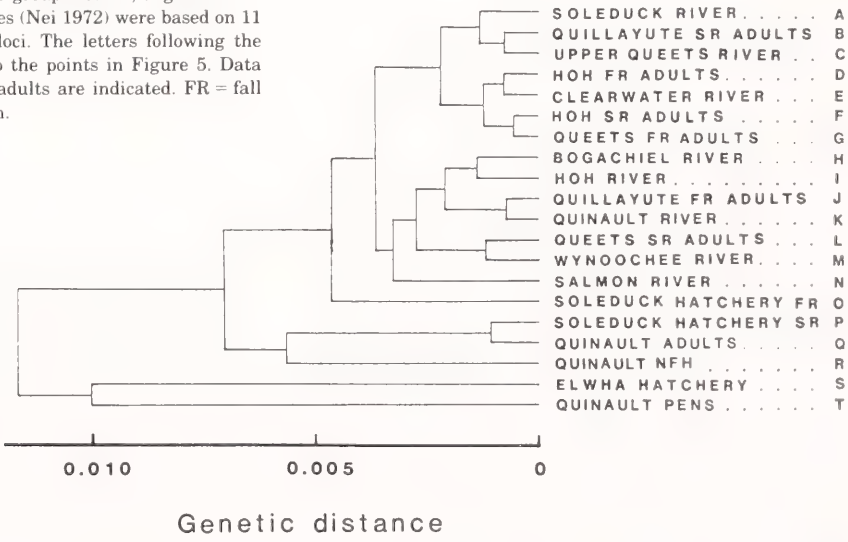


FIGURE 3b.—Chinook salmon—common-allele frequencies (q) for three protein-coding loci, or pairs of loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not presented and were not used in the analyses. Data for Gpi-2 were not included in the ANOVA because of missing data (see Appendix Table A1). H. = hatchery; Ad. = adults; F = fall run; SP/SU = mixed spring/summer run; SU = summer run. Adults were from the fall run unless specified otherwise.

FIGURE 4.—Chinook salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances (Nei 1972) were based on 11 protein-coding loci or pairs of loci. The letters following the names of samples correspond to the points in Figure 5. Data were from juvenile fish unless adults are indicated. FR = fall run; SR = spring or summer run.



most similar to wild fish. Summer-run adults and fall-run adults from the Quillayute River both clustered with the wild fish, suggesting that a large proportion of the fish in these samples were wild fish. Multidimensional scaling gave similar results and more clearly illustrated that hatchery populations were distinct not only from the wild fish but also from each other (Fig. 5).

Coho Salmon

Coho salmon showed genic variability at 21 loci or pairs of loci; however, the frequency of the common allele was <0.95 for most samples at only 2 loci: *bGala-2* and *Idh-3,4* (Fig. 6, App. Table 2). Allendorf and Utter (1979) found a similar lack of variation, reporting that coho salmon display the least amount of electrophoretic variation of the five Pacific salmon species in North America.

Hierarchical analysis of genic diversity (heterozygosity) showed that the interbrood level accounted for 2% (= 0.09/(0.09 + 0.85 + 3.97; Table 6) of the genic diversity observed among samples of coho salmon; the within-drainage level accounted for 17% and the interdrainage level for 81%. Variation at *Pnp-1* had a substantial influence on the average locus values. Unfortunately, data for *Pnp-1* were missing for several of the samples because the methodology for this enzyme was not stabilized until we were well into our study. With *Pnp-1* excluded from the analysis, the interbrood level accounted for 5% of the genic diversity observed among samples, the within-drainage level accounted for 39%, and the interdrainage level accounted for 56%.

Variation in allele frequencies among streams within the Quillayute and Queets drainages was statistically significant (tested at *bGala-2, Idh-3,4*, and *Pnp-1*; $G = 11.27$ with 5 degrees of freedom; $P < 0.05$); however, interpretation of this result is complicated because data were not available to adequately account for variation among year classes. Variation among drainages was not significantly greater than variation within drainages ($P > 0.10$, hierarchical likelihood ratio

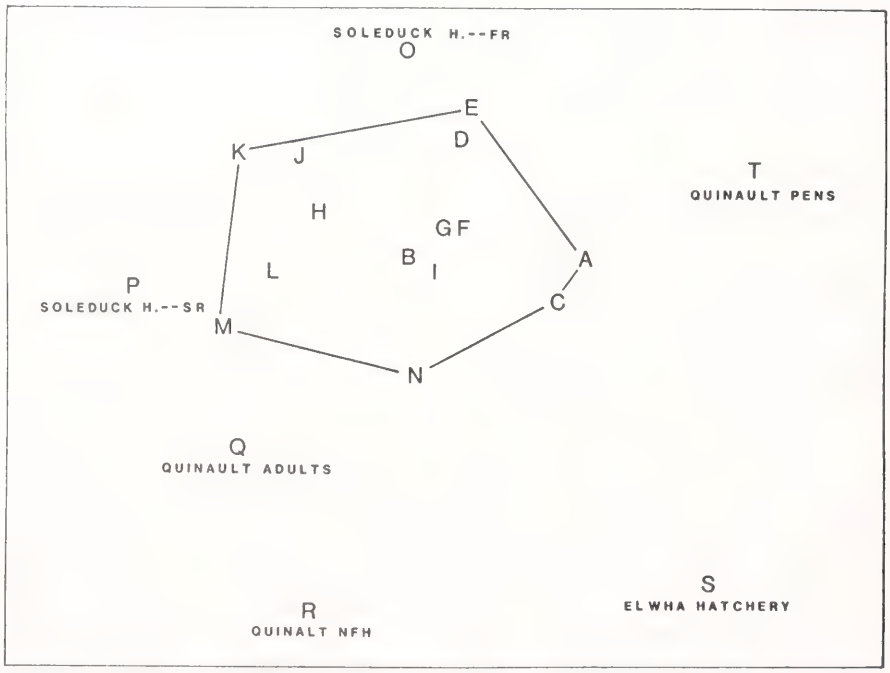


FIGURE 5.—Chinook salmon—two-dimensional representation (from multidimensional scaling) of genetic distances among samples collected for this study. The letters correspond to the groups identified in Figure 4. The polygon encloses the samples of wild fish (A through N). The aim of multidimensional scaling is to represent each group by a point in two-dimensional space so that the relative distances among points represent the relative (genetic) distances between groups.

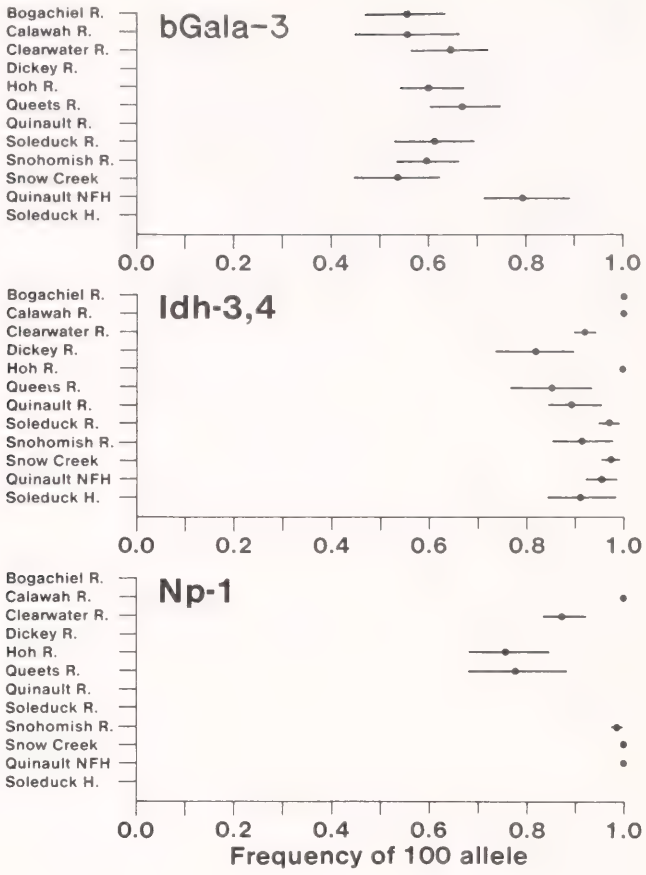


FIGURE 6.—Coho salmon—common-allele frequencies (q) for several protein-coding loci. Each horizontal bar is $4\sqrt{q(1-q)/2n}$ in length and approximates the 95% confidence interval; n = number of fish scored. Frequencies for fewer than 25 fish are not shown and were not used in analysis.

TABLE 6.—Coho salmon—hierarchical analysis of electrophoretically detectable gene diversity for coho salmon from the Quillayute, Hoh, Queets, Quinault and Wynoochee Rivers. Analysis was based on 58 loci, including 36 that were monomorphic. The hierarchical design is shown in Figure 3.

Locus	Total gene diversity (H_T)	Relative gene diversity (%)			
		Within samples	Among broods	Within drainages	Among drainages
Average	0.021	95.09	0.09	0.85	3.97
Average excluding *Pnp-1*	0.016	97.64	0.12	0.93	1.31

analysis; Grant et al. 1980; Smouse and Ward 1978).

Samples without data for *bGala-1* or *Idh-3,4*, the most variable loci, were omitted from the UPGM cluster analysis (Fig. 7) and multidimensional scaling (Fig. 8). Both analyses showed that fish from Quinault NFH were distinct from wild fish; much of this distinctiveness occurred at the *bGala-2* locus (Fig. 6). Fish from Snow Creek and the Snohomish River clustered among the wild fish from the north coast. The results were similar when *Pnp-1* was excluded from the analysis, except that fish from the upper Queets River were no longer distinct from the other wild fish.

DISCUSSION

Wild Populations

Variation in allele frequencies among drainages for chinook salmon was not statistically significant. The inability to detect differences among drainages could have resulted from 1) low statistical power (probability of rejecting H_0 if it is false) because we had too few broods or because variation in racial composition of juveniles in different years inflated the estimates of error variance, 2) our exclusive reliance on data for genes that can be sampled by electrophoresis, or 3) a lack of true genetic difference among groups. We

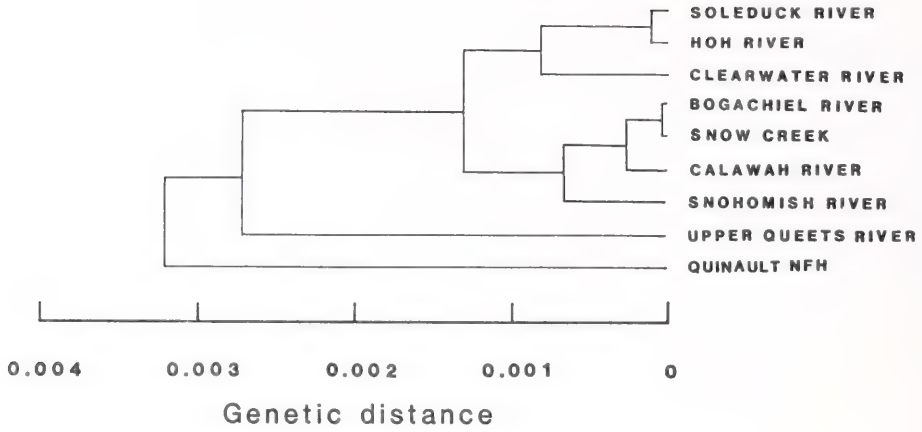


FIGURE 7.—Coho salmon—dendrogram showing results of analysis, by the unweighted pair group method, of genetic distance between samples. Distances were based on 24 protein-coding loci or pairs of loci.

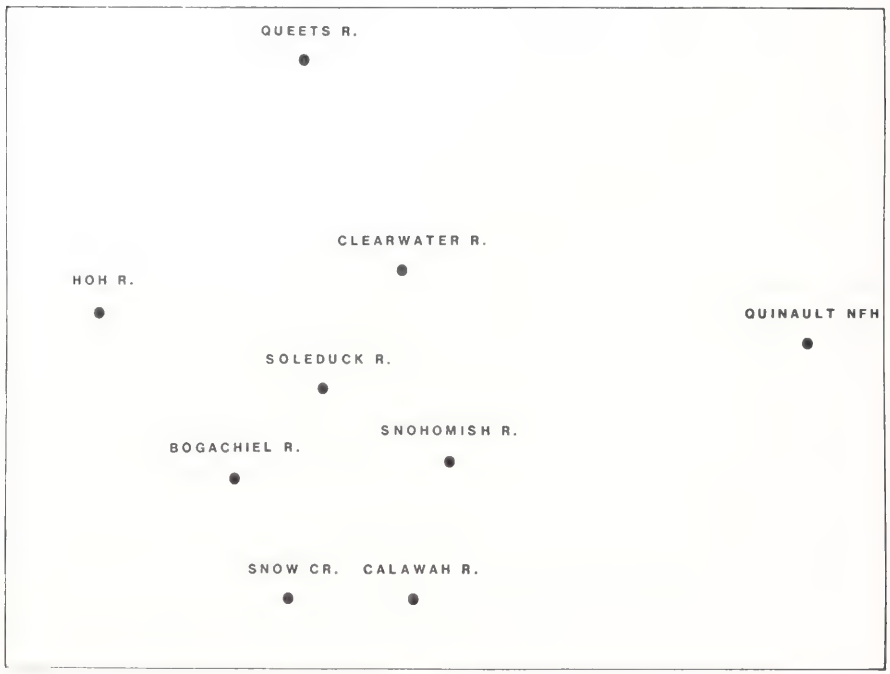


FIGURE 8.—Coho salmon—two-dimensional representation (from nonmetric multidimensional scaling) of genetic distances among samples collected for this study. Only samples scored for *bGala-2* and *Idh-3,4* were included in the analysis.

emphasize that the lack of differentiation in frequencies of electrophoretically detectable alleles does not preclude the existence of important genetic differences or status as separate stocks (genetic populations). The high degree of "homing" by both chinook salmon (see, e.g., Rich and Holmes 1928) and coho salmon (see, e.g., Shapavalov and Taft 1954) to the streams from which they originate suggests that salmon from different drainages should be considered as separate

stocks unless strong evidence exists to the contrary.

Our data suggested that summer chinook salmon were distinct from fall chinook salmon ($P = 0.06$, Table 5). Electrophoretic differences between distinct runs or life history types of chinook salmon were also found within the Nanaimo River system (Carl and Healey 1984) and within the Columbia River system (Kristiansson and McIntyre 1976). Summer-run fish from different streams along the north coast were not sufficiently similar to form a cluster separate from the fall-run fish (Figs. 4, 5), and the differences among populations of summer-run fish may be as great as the differences between summer- and fall-run fish. Unfortunately the small number of populations precluded rigorous comparison of these differences.

The (significant) variation in allele frequencies between year classes of juvenile chinook salmon may have been exaggerated by variation between years in the proportion of fish from the three different runs. This possibility illustrates the need for sampling adult chinook salmon (only adults can be distinguished according to run) in river systems where juveniles from different runs occur together. Of course, the utility of sampling adults to genetically describe wild populations is compromised if adult hatchery and wild fish occur together and cannot be reliably separated.

The gene diversity analysis for coho salmon showed that diversity within drainages was eight to nine times the diversity among broods, with or without *Pnp-1* included in the analysis, and suggested that separate breeding units exist within drainages as well as between drainages. Separate breeding units within drainages were also suggested by the likelihood ratio analysis.

Hatchery Fish Versus Wild Fish

Analysis of variance for hatchery and wild chinook salmon, and the cluster analyses for both chinook and coho salmon showed that the hatchery populations of the north coast were genetically distinct from the populations of wild fish. Indeed, coho salmon from Snow Creek or from the Snohomish River were more similar to wild coho salmon from the north coast than were coho salmon from Quinault National Fish Hatchery (Fig. 7).

The differences between hatchery and wild fish were to be expected because the hatchery populations were developed with fish from locations in addition to the local stream or exclusive of the local stream. Among chinook salmon, fall-run fish at Soleduck Hatchery were the most similar to wild fish (Fig. 5), probably because the Soleduck Hatchery population was the only hatchery population developed primarily with local fish (Houston fn. 3). Fall coho salmon at Soleduck Hatchery were also primarily developed with local fish but were not included in the analysis because of missing data. We would expect these coho salmon to be more similar to wild fish than were the coho salmon from Quinault National Fish Hatchery—and that expectation held for allele frequencies at *Ada-2* and *Ldh-4*, and was not countered by evidence from any other loci (App. Table A2).

It is reasonable to assume that interbreeding with fall chinook salmon (or fall coho salmon) from Soleduck Hatchery will cause less reduction of fitness and less genetic change for wild fish than will interbreeding with the other (less similar) hatchery fish (Helle 1981; Reisenbichler 1984). The observed differences between fall chinook salmon at Soleduck Hatchery and wild fish probably exist because few wild fish are included in the hatchery brood stock. Data for steelhead, *Salmo gairdneri*, (Reisenbichler and Phelps 1985[5]) illustrate that the continued use of wild fish in the hatchery brood stock and avoidance of selective breeding are necessary to maintain a hatchery population that is genetically similar to wild fish. Where hatchery populations can be managed separately from wild populations and where few hatchery fish stray onto natural spawning areas, perhaps there is little reason to ensure that hatchery fish are genetically similar to wild fish. However, where substantial numbers of hatchery fish successfully spawn in streams and where genetic resources are to be conserved, hatchery fish should be as genetically similar as possible to the wild fish (e.g., Helle 1981).

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[5]Reisenbichler, R. R., and S. R. Phelps. 1985. Genetic structure of steelhead, *Salmo gairdneri*, from the north coast of Washington State. Unpubl. rep. National Fishery Research Center, Seattle, WA.

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APPENDIX TABLE 1.—Allele frequencies for chinook salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample names correspond to locations shown in Figure 1.

			Ah-3				*Adh-1*		*Gpi-2*			
Location and sample	Brood	*N*	100	85	118	108	−100	−50	100	67	−15	150
Quillayute River												
1 Fall-run adults	[1](1983)	99	0.892	0.097	0.011	—	0.990	0.010	0.714*	0.276*	0.010	—
1 Summer-run adults	[1](1983)	120	0.906	0.094	—	—	0.996	0.004	—	—	—	—
3 Soleduck River	1981	70	0.884	0.101	0.014	—	0.971	0.029	—	—	—	—
	1982	40	0.971	0.029	—	—	—	—	0.462	0.488	0.010	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982		0.840	0.130	—	0.030	0.990	0.010	—	—	—	—
	1982	40	—	—	—	—	—	—	0.662	0.288	0.012	0.038
Spring/summery run	[2]pre-1982		0.850	0.150	—	—	0.980	0.020	—	—	—	—
	1982	50	0.830	0.170	—	—	1.000	—	0.700	0.300	—	—
	[1](1983)	77	0.889	0.111	—	—	1.000	—	0.761	0.239	—	—
6 Bogachiel River	1981	70	0.926	0.066	0.008	—	0.985	0.015	—	—	—	—
	1982	40	0.894	0.091	—	0.015	—	—	0.650	0.338	—	0.012
Hoh River												
7 Fall-run adults	[1](1983)	37	0.957	0.043	—	—	0.973	0.027	0.650	0.350	—	—
7 Summer-run adults	[1](1983)	86	0.983	0.017	—	—	0.960	0.040	0.574	0.426	—	—
8 Juveniles	1981	70	0.900	0.064	0.036	—	0.991	0.009	—	—	—	—
	1982	76	0.950	0.029	0.021	—	—	—	0.592	0.388	0.020	—
Queets River												
9 Fall-run adults	[1](1983)	94	0.944	0.044	0.012	—	0.978	0.022	0.595	0.399	0.006	—
9 Summer-run adults	[1](1983)	60	0.907	0.074	0.019	—	0.969	0.031	0.652	0.348	—	—
10 Clearwater River	1981	70	0.891	0.094	0.014	—	0.957	0.043	—	—	—	—
	1982	48	0.917	0.052	0.031	—	0.980	0.020	0.650	0.350	—	—
12 Salmon River	1982	48	0.880	0.109	0.011	—	0.943	0.057	0.531	0.469	—	—
11 Upper Queets River	1981	70	0.906	0.087	0.007	—	0.957	0.043	—	—	—	—
	1982	54	0.880	0.070	0.050	—	—	—	0.491	0.500	0.009	—
Quinault River												
13 Adults	[1](1983)	64	0.927	0.073	—	—	0.976	0.024	—	—	—	—
14 Lower Quinault River	1982	55	—	—	—	—	—	—	0.750	0.236	0.014	—
17 Upper Quinault River	1982	53	0.904	0.096	—	—	—	—	—	—	—	—
15 Quinault NFH	[2]pre-1982	99	0.920	0.080	—	—	0.980	0.020	—	—	—	—
	1982	50	0.958	0.042	—	—	1.000	—	0.411	0.589	—	—
16 Quinault Pens	1982	50	0.870	0.054	0.076	—	1.000	—	0.500	0.500	—	—
Others												
18 Wynoochee River	1982	66	—	—	—	—	—	—	0.635	0.365	—	—
21 Elwha Spawning Channel	1981	39	—	—	—	—	—	—	0.500	0.500	—	—
	1982	40	0.962	0.038	—	—	1.000	—	0.237	0.745	—	—

[1]Offspring from these adults would have belonged to the 1983 year class.

[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Iddh-1,2*		*Idh-3,4*				*Mdh-1,2*		*Mdh-3,4*		
		100	36	100	120	87	60	100	120	100	115	67
Quillayute River												
1 Fall-run adults	[1](1983)	—	—	0.976	0.024	—	—	1.000	—	0.980	0.020	—
1 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.971	0.025	0.004
3 Soleduck River	1981	—	—	0.911	0.057	0.032	—	0.987	0.013	0.993	0.007	—
	1982	—	—	1.000	—	—	—	1.000	—	0.975	0.025	—
4 Soleduck Hatchery												
Fall run	[2]pre-1982	—	—	0.990	0.010	—	—	1.000	—	0.990	0.010	—
	1982	—	—	1.000	—	—	—	1.000	—	0.938	0.062	—
Spring/summer run	[2]pre-1982	—	—	0.955	0.035	0.010	—	1.000	—	0.975	0.015	0.010
	1982	—	—	0.985	0.010	0.005	—	1.000	—	0.985	0.015	—
	[1](1983)	—	—	0.915	0.078	0.003	0.004	1.000	—	0.987	0.006	0.007
6 Bogachiel River	1981	—	—	0.946	0.054	—	—	1.000	—	0.975	0.025	—
	1982	—	—	1.000	—	—	—	1.000	—	0.888	0.112	—
Hoh River												
7 Fall-run adults	[1](1983)	—	—	0.910	0.090	—	—	1.000	—	0.959	0.041	—
7 Summer-run adults	[1](1983)	—	—	0.922	0.078	—	—	1.000	—	0.973	0.027	—
8 Juveniles	1981	—	—	0.929	0.071	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.996	0.004	—	—	1.000	—	0.990	0.010	—
Queets River												
9 Fall-run adults	[1](1983)	—	—	0.915	0.085	—	—	1.000	—	0.979	0.021	—
9 Summer-run adults	[1](1983)	—	—	0.928	0.072	—	—	1.000	—	0.992	0.008	—
10 Clearwater River	1981	—	—	0.903	0.060	0.037	—	1.000	—	0.961	0.039	—
	1982	0.897	0.103	0.825	0.175	—	—	1.000	—	0.970	0.025	0.005
12 Salmon River	1982	—	—	0.938	0.062	—	—	0.990	0.010	0.974	0.026	—
11 Upper Queets River	1981	—	—	0.873	0.127	—	—	1.000	—	0.996	0.004	—
	1982	—	—	0.936	0.064	—	—	1.000	—	0.995	0.005	—
Quinault River												
13 Adults	[1](1983)	—	—	0.952	0.048	—	—	1.000	—	0.988	—	0.012
14 Lower Quinault River	1982	—	—	0.943	0.057	—	—	1.000	—	0.991	0.009	—
17 Upper Quinault River	1982	—	—	0.931	0.069	—	—	1.000	—	0.990	0.010	—
15 Quinault NFH	[2]pre-1982	—	—	0.900	0.090	0.010	—	1.000	—	0.990	0.010	—
	1982	—	—	0.974	0.026	—	—	1.000	—	1.000	—	—
16 Quinault Pens	1982	—	—	0.978	0.022	—	—	1.000	—	0.995	0.005	—
Others												
18 Wynoochee River	1982	—	—	0.980	0.020	—	—	1.000	—	0.996	0.004	—
21 Elwha Spawning Channel	1981	—	—	0.894	0.106	—	—	1.000	—	0.929	—	0.071
	1982	0.938	0.062	0.950	0.050	—	—	1.000	—	1.000	—	—

[1]Offspring from these adults would have belonged to the 1983 year class

[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Mpi-1*			*Pgm-1*			*Pgdh-1*		*Pgk-2*	
		100	116	90	100	129	150	100	90	100	81
Quillayute River											
1 Fall-run adults	[1](1983)	0.672	0.328	—	0.909	0.091	—	1.000	—	0.512	0.488
1 Summer-run adults	[1](1983)	0.688	0.312	—	0.951	0.049	—	1.000	—	0.475	0.525
3 Soleduck River	1981	0.743	0.257	—	0.936	0.064	—	1.000	—	0.486	0.514
	1982	0.650	0.350	—	0.962	0.038	—	1.000	—	0.325	0.675
4 Soleduck Hatchery											
Fall run	[2]pre-1982	0.810	0.190	—	1.000	—	—	1.000	—	0.370	0.630
	1982	0.862	0.138	—	0.988	0.012	—	1.000	—	—	—
Spring/summer run	[2]pre-1982	0.620	0.370	0.010	1.000	—	—	1.000	—	0.490	0.510
	1982	0.580	0.410	0.010	0.990	0.010	—	1.000	—	0.610	0.390
	[1](1983)	0.753	0.247	—	0.980	0.020	—	1.000	—	0.617	0.383
6 Bogachiel River	1981	0.621	0.379	—	0.949	0.022	0.029	1.000	—	0.543	0.457
	1982	0.663	0.337	—	0.925	0.075	—	1.000	—	0.487	0.513
Hoh River											
7 Fall-run adults	[1](1983)	0.743	0.257	—	0.946	0.054	—	1.000	—	0.405	0.595
7 Summer-run adults	[1](1983)	0.738	0.262	—	0.886	0.114	—	1.000	—	0.473	0.527
8 Juveniles	1981	0.593	0.407	—	0.900	0.086	0.014	1.000	—	0.470	0.530
	1982	0.669	0.331	—	0.954	0.039	0.007	1.000	—	0.454	0.546
Queets River											
9 Fall-run adults	[1](1983)	0.704	0.296	—	0.914	0.086	—	1.000	—	0.467	0.533
9 Summer-run adults	[1](1983)	0.661	0.339	—	0.882	0.118	—	1.000	—	0.591	0.409
10 Clearwater River	1981	0.732	0.268	—	0.943	0.050	0.007	1.000	—	0.421	0.579
	1982	0.775	0.225	—	0.843	0.147	0.010	1.000	—	0.438	0.562
12 Salmon River	1982	0.638	0.362	—	0.906	0.052	0.042	1.000	—	0.562	0.438
11 Upper Queets River	1981	0.636	0.364	—	0.864	0.079	0.057	1.000	—	0.369	0.631
	1982	0.750	0.250	—	0.991	0.009	—	1.000	—	0.463	0.537
Quinault River											
13 Adults	[1](1983)	0.746	0.254	—	0.984	0.016	—	0.992	0.008	0.597	0.403
14 Lower Quinault River	1982	0.632	0.368	—	0.864	0.136	—	1.000	—	0.539	0.461
17 Upper Quinault River	1982	0.654	0.346	—	0.896	0.104	—	1.000	—	0.500	0.500
15 Quinault NFH	[2]pre-1982	0.610	0.390	—	0.930	0.050	0.020	—	—	0.580	0.420
	1982	0.786	0.214	—	0.970	0.030	—	0.980	0.020	0.776	0.224
16 Quinault Pens	1982	0.730	0.270	—	0.940	0.040	0.020	1.000	—	0.235	0.765
Others											
18 Wynoochee River	1982	0.723	0.269	0.008	0.917	0.083	—	1.000	—	0.632	0.368
21 Elwha Spawning Channel	1981	0.500	0.482	0.018	0.987	—	0.013	1.000	—	0.468	0.532
	1982	0.632	0.368	—	1.000	—	—	1.000	—	0.250	0.750

[1]Offspring from these adults would have belonged to the 1983 year class.

[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 1.—*Continued.*

Location and sample	Brood	*Sod-1* −100	*Sod-1* −225	*Sod-1* 400
Quillayute River				
1 Fall-run adults	[1](1983)	0.904	0.096	—
1 Summer-run adults	[1](1983)	0.860	0.140	—
3 Soleduck River	1981	0.903	0.097	—
	1982	0.975	0.025	—
4 Soleduck Hatchery				
Fall run	[2]pre-1982	0.800	0.200	—
	1982	0.833	0.167	—
Spring/summer run	[2]pre-1982	0.620	0.380	—
	1982	0.840	0.160	—
	[1](1983)	0.724	0.276	—
6 Bogachiel River	1981	0.885	0.115	—
	1982	0.926	0.074	—
Hoh River				
7 Fall-run adults	[1](1983)	0.892	0.108	—
7 Summer-run adults	[1](1983)	0.879	0.121	—
8 Juveniles	1981	0.886	0.114	—
	1982	0.868	0.132	—
Queets River				
9 Fall-run adults	[1](1983)	0.919	0.081	—
9 Summer-run adults	[1](1983)	0.852	0.148	—
10 Clearwater River	1981	0.913	0.080	0.007
	1982	0.907	0.093	—
12 Salmon River	1982	0.927	0.073	—
11 Upper Queets River	1981	0.886	0.107	0.007
	1982	0.861	0.139	—
Quinault River				
13 Adults	[1](1983)	0.703	0.297	—
14 Lower Quinault River	1982	0.949	0.051	—
17 Upper Quinault River	1982	0.824	0.176	—
15 Quinault NFH	[2]pre-1982	0.780	0.210	0.010
	1982	0.720	0.200	0.080
16 Quinault Pens	1982	0.929	0.071	—
Others				
18 Wynoochee River	1982	0.821	0.179	—
21 Elwha Spawning Channel	1981	0.741	0.259	—
	1982	0.697	0.303	—

[1]Offspring from these adults would have belonged to the 1983 year class.
[2]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study; final report of research. Unpubl. rep. Natl. Mar. Fish. Serv., NOAA, Seattle, WA.

APPENDIX TABLE 2.—Allele frequencies for coho salmon from Washington. Each allele is designated by its mobility (relative to the common allele) times 100. *N* is the number of fish scored for most loci; however, fewer fish may have been scored at some loci. Frequencies from fewer than *N*/2 fish are identified with an asterisk, and frequencies from fewer than 25 fish are not shown and were not used in our analyses. Numbers preceding sample name correspond to locations shown in Figure 1.

			bGala-2		*Ah-3*				*Ada-2*			*Aat-3,4*	
	Brood	*N*	100	128	100	91	115	130	100	110	91	100	87
Quillayute River													
2 Dickey River	1981	52	—	—	0.990	—	—	0.010	0.990	0.010	—	1.000	—
3 Soleduck River	1981	37	0.660	0.340	0.973	0.027	—	—	0.933	0.967	—	1.000	—
	1982	48	0.583	0.417	1.000	—	—	—	1.000	—	—	1.000	—
4 Soleduck Hatchery	1981	40	—	—	0.988	0.012	—	—	1.000	—	—	1.000	—
5 Calawah River	1982	40	0.551	0.449	0.925	0.050	0.025	—	0.988	0.013	—	1.000	—
6 Bogachiel River	1982	74	0.546	0.454	1.000	—	—	—	1.000	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	48	0.061	0.399	1.000	—	—	—	0.990	0.010	—	1.000	—
Pin Creeks	1982	44	—	—	0.989	0.011	—	—	1.000	—	—	1.000	—
8 Other tributaries	1982	45	0.616	0.384	1.000	—	—	—	1.000	—	—	1.000	—
Queets River													
10 Clearwater River	1981	210	0.637*	0.363	0.979	0.021	—	—	0.995	0.005	—	1.000	—
11 Upper Queets River	1981	76	0.674	0.326	1.000	—	—	—	0.993	0.007	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	60	—	—	—	—	—	—	1.000	—	—	0.923	0.077
15 Quinault NFH	1981	40	—	—	1.000	—	—	—	0.961	0.039	—	1.000	—
	1982	40	0.814	0.186	0.988	0.012	—	—	0.988	—	0.012	1.000	—
Others													
19 Snohomish River	1981, 1982	106	0.595	0.405	0.986	0.009	0.005	—	1.000	—	—	1.000	—
20 Snow Creek	1981	60	0.542	0.458	1.000	—	—	—	—	—	—	1.000	—

		Ck-1		*Gpi-1*		*Gpi-2*			*Gpi-3*		*G3pdh-1*	
	Brood	100	127	100	250	100	157	67	100	90	−100	−15
Quillayute River												
2 Dickey River	1981	1.000	—	1.000	—	0.990	0.010	—	1.000	—	0.990	0.010
3 Soleduck River	1981	1.000	—	1.000	—	0.986	0.014	—	1.000	—	1.000	—
	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.969	0.031
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	0.987	0.013
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Hoh River												
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	1.000	—	0.989	0.011	—	1.000	—	1.000	—
Queets River												
10 Clearwater River	1981	1.000	—	0.998	0.002	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	1.000	—	0.993	0.007	0.993	—	0.007	1.000	—	0.987	0.013
Quinalt River												
13 Lower Quinault River	1982	1.000	—	1.000	—	0.991	0.009	—	1.000	—	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.959	0.041
	1982	1.000	—	1.000	—	0.950	0.050	—	0.975	0.025	1.000	—
Others												
19 Snohomish River	1981, 1982	0.995	0.005	1.000	—	0.981	—	0.019	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	—	1.000	—	0.992	0.008

APPENDIX TABLE 2.—*Continued.*

		Idh-3,4					*Ldh-3*			*Ldh-4*		*Lgl-1*	
	Brood	100	130	70	123	157	100	45	140	100	110	100	80
Quillayute River													
2 Dickey River	1981	0.825	0.169	0.006	—	—	0.971	0.029	—	1.000	—	1.000	—
3 Soleduck River	1981	0.973	—	0.007	0.020	—	0.986	—	0.014	1.000	—	1.000	—
	1982	—	—	—	—	—	1.000	—	—	1.000	—	1.000	—
4 Soleduck Hatchery	1981	0.964	0.036	—	—	—	1.000	—	—	1.000	—	1.000	—
5 Calawah River	1982	1.000	—	—	—	—	1.000	—	—	1.000	—	0.963	0.037
6 Bogachiel River	1982	0.996	—	0.004	—	—	0.993	—	0.007	1.000	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	0.995	—	0.005	—	—	1.000	—	—	1.000	—	1.000	—
Pin Creeks	1982	0.978	—	0.022	—	—	0.988	0.012	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	—	—	0.989	0.011	—	1.000	—	1.000	—
Queets River													
10 Clearwater River	1981	0.924	0.073	0.001	0.002	—	0.993	0.007	—	1.000	—	1.000	—
11 Upper Queets River	1981	0.858*	0.132*	—	0.006*	0.004*	1.000	—	—	0.994	0.006	1.000	—
Quinalt River													
13 Lower Quinault River	1982	0.905	0.095	—	—	—	1.000	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	0.917	0.077	—	—	0.006	1.000	—	—	1.000	—	1.000	—
	1982	1.000	—	—	—	—	0.988	0.012	—	0.975	0.025	1.000	—
Others													
19 Snohomish River	1981, 1982	0.920	0.070	0.007	—	0.003	1.000	—	—	0.972	0.028	1.000	—
20 Snow Creek	1981	0.985	0.015	—	—	—	1.000	—	—	1.000	—	1.000	—

		Mdh-1,2			*Mdh-3,4*					*Mdh-5*		*MdhP-1*	
	Brood	100	37	210	100	123	110	89	140	100	107	100	130
Quillayute River													
2 Dickey River	1981	1.000	—	—	0.991	0.009	—	—	—	0.971	0.029	1.000	—
3 Soleduck River	1981	1.000	—	—	0.967	0.020	—	—	0.013	—	—	1.000	—
	1982	1.000	—	—	1.000	—	—	—	—	—	—	—	—
4 Soleduck Hatchery	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—
5 Calawah River	1982	1.000	—	—	0.988	0.012	—	—	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	—	0.993	0.007	—	—	—	—	—	1.000	—
Hoh River													
8 Winfield, Nolan,	1981	1.000	—	—	0.985	0.005	0.010	—	—	1.000	—	1.000	—
Pin Creeks	1982	1.000	—	—	0.955	0.040	—	0.006	—	1.000	—	1.000	—
8 Other tributaries	1982	1.000	—	—	0.956	0.044	—	—	—	—	—	1.000	—
Queets River													
10 Clearwater River	1981	1.000	—	—	0.985	0.010	—	0.005	—	0.960	0.040	0.990	0.010
11 Upper Queets River	1981	0.994	0.003	0.003	0.997	0.003	—	—	—	1.000*	—	1.000	—
Quinalt River													
13 Lower Quinault River	1982	1.000	—	—	1.000	—	—	—	—	1.000	—	1.000	—
15 Quinault NFH	1981	1.000	—	—	1.000	—	—	—	—	0.950	0.050	1.000	—
	1982	1.000	—	—	0.994	0.006	—	—	—	—	—	1.000	—
Others													
19 Snohomish River	1981, 1982	0.997	0.003	—	0.998	0.002	—	—	—	1.000	—	1.000	—
20 Snow Creek	1981	1.000	—	—	1.000	—	—	—	—	—	—	1.000	—

APPENDIX TABLE 2.—*Continued.*

	Brood	*Mpi-1*		*Pgm-2*		*Pgdh-1*		*Pnp-1*	
		100	123	−100	−55	100	92	100	155
Quillayute River									
2 Dickey River	1981	1.000	—	0.990	0.010	1.000	—	—	—
3 Soleduck River	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	—	—
4 Soleduck Hatchery	1981	1.000	—	1.000	—	1.000	—	—	—
5 Calawah River	1982	1.000	—	1.000	—	1.000	—	1.000	—
6 Bogachiel River	1982	1.000	—	1.000	—	1.000	—	—	—
Hoh River									
8 Winfield, Nolan,	1981	1.000	—	1.000	—	1.000	—	—	—
Pin Creeks	1982	1.000	—	1.000	—	1.000	—	0.673	0.327
8 Other tributaries	1982	1.000	—	1.000	—	1.000	—	—	—
Queets River									
10 Clearwater River	1981	0.995	0.005	1.000	—	1.000	—	0.877*	0.123*
11 Upper Queets River	1981	1.000	—	1.000	—	1.000	—	0.780*	0.220*
Quinault River									
13 Lower Quinault River	1982	1.000	—	1.000	—	0.974	0.026	—	—
15 Quinault NFH	1981	1.000	—	1.000	—	1.000	—	—	—
	1982	1.000	—	1.000	—	1.000	—	1.000	—
Others									
19 Snohomish River	1981, 1982	1.000	—	1.000	—	1.000	—	0.995	0.005
20 Snow Creek	1981	1.000	—	1.000	—	1.000	—	1.000	—

ASSESSMENT OF INTERACTION BETWEEN NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, FISHERIES BY USE OF A SIMULATION MODEL

P. KLEIBER AND B. BAKER[1]

ABSTRACT

Using a simulation model of a typical year in the North Pacific albacore fisheries in the 1970s, we tested for the degree to which the activity of fleets affects the performance of other fleets. The results show that rather drastic (factor of two) changes in the activity of any of the three principal albacore fleets have only a mild effect on the catch of the other fleets. With the overall exploitation rate in the model close to the exploitation rate determined from tagging results (6%), the maximum degree of interaction was a 7.5% drop in longline catch resulting from doubling the baitboat effort. The mild degree of interaction was insensitive to exploitation rate up to approximately 10% exploitation, although interaction became more severe at higher levels of exploitation.

Fishery interaction, the effect of one fishing fleet on another, is a phenomenon of growing concern to those involved in the management and development of pelagic fisheries. This concern has arisen from the growing awareness that oceanic fishery resources are not unlimited and from the evolution of exclusive economic zones to protect local interests against large international fishing fleets. Assessing the potential for interaction between tuna fisheries in different island countries was one of the principal reasons that the South Pacific Commission conducted the Skipjack Survey and Assessment Programme (Kearney 1983). Workshops on this topic have been held during international tuna fishery meetings, and a Tuna Fisheries Interaction Programme has been proposed within the Indo-Pacific Tuna Development and Management Programme.

Because there is a multiplicity of fleets and nations involved in harvesting albacore, *Thunnus alalunga*, a tuna, in the North Pacific, there is a potential concern about interaction between these fleets. A history of North Pacific albacore fishing since the 1950s is summarized by Laurs (1983). Three principal fleets have been responsible for the catch: the Japanese baitboat, the Japanese longline, and the United States jigboat fleets (Fig. 1). In the 1970s these accounted for more than 90% (60%, 15%, and 18%, respectively) of the total catch. In recent years, Japanese gill net gear has become important, accounting for approximately 20% of the total catch from 1981 through 1983 (Fig. 1). Detailed statistics on this emerging fishery are not currently available.

Among the three principal fleets, the U.S. fleet tends to take the smallest fish, and the longline the largest, but the size distributions in the catch overlap to a large extent (Fig. 2). The geographic distribution of the fleets is indicated in Figure 3, but the overlap is overemphasized because there is seasonal separation in many cases. Nevertheless, the migratory nature of albacore makes for potentially significant interaction between fleets that are separated in time and space.

Because there have been no clear trends in catch or in catch per effort (Laurs 1983), it has been assumed that the albacore stocks have not been adversely affected by the fisheries, and such woes as the fishermen have had have not been blamed on poor status of stocks. Therefore there has been little reason for fleets to accuse one another of depleting the stocks and thus little concern about fishery interaction. To verify that sanguine view, we have estimated the degree of interaction between the three principal albacore fisheries in the North Pacific. We defined interaction to be the degree to which changes in the activity (effort) of one fleet affect the performance (catch) of another fleet. The magnitude of this kind of interaction cannot be calculated directly from fishery data, nor can controlled, real-life experiments be conducted on the grand scale necessary to address this topic. However, experiments conducted on simulation model are feasible. The results of such experiments with an

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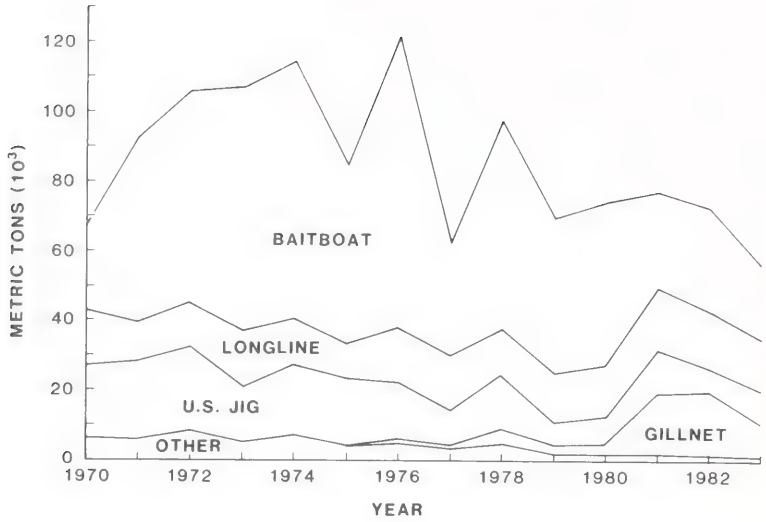

FIGURE 1.—Annual catch of albacore by gear type. [Data from Majors and Miller. 1985. Summary of the 1984 North Pacific albacore fishery data. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Admin. Rep. LJ-85-14, 45 p.]

albacore simulation model are the subject of this report.

THE MODEL

We used a model that incorporates recruitment, growth, migration, natural mortality, and harvest of albacore by the Japanese baitboat fleet, the Japanese longline fleet, and the United States surface fleet (primarily jig gear). Our approach was to manipulate the effort of one fleet at a time and note the effect on the catch of the other fleets.

A full technical description of the model is given by Kleiber and Baker[2]. We discretized fish size into 5 cm length classes and the North Pacific range of albacore into nine geographic zones (Fig. 3). The basic dynamics within a size class and zone are described by the following differential equation:

$$\frac{dP_{s,z}(t)}{dt} = G_{s-1} P_{s-1,z}(t) + \sum_{\hat{z}} \mu_{\hat{z}\to z} P_{s,\hat{z}}(t)$$

$$- \left[M + G_s + \sum_{\hat{z}} \mu_{z\to\hat{z}} \right] P_{s,z}(t) - \sum_{g} c_{s,z,g}$$

where $c_{s,z,g} = q_{s,g} f_{z,g}(t) P_{s,z}(t)$ is the catch rate (number per unit time) by size, zone, and gear. The symbols are defined as follows:

s —index for size class
z —index for geographic zone
$\hat{z}$ —index for zone adjacent to z
g —index for gear type
$P_{s,z}(t)$ —population (numbers) by size and zone at time t

the following being input parameters:

$P_{0,z}(t)$ —recruitment rate by zone at time t
G_s —proportion growing out of size s per unit time
G_0 —always = 1 (so that $P_{0,z}(t)$ is recruitment rate)
$\mu_{z_1\to z_2}$ —coefficient of migration from zone z_1 to zone z_2
M —natural mortality
$q_{s,g}$ —catchability by size and gear
$f_{z,g}(t)$ —effort by zone and gear at time t.

INPUT PARAMETER VALUES

Full details of how input parameters were estimated are given by Kleiber and Baker (fn. 2). The following is a summary.

The most complete catch and effort data sets that were available to us and that cover the three

[2]Kleiber, P., and B. Baker. 1987. The North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-87-2, 38 p.

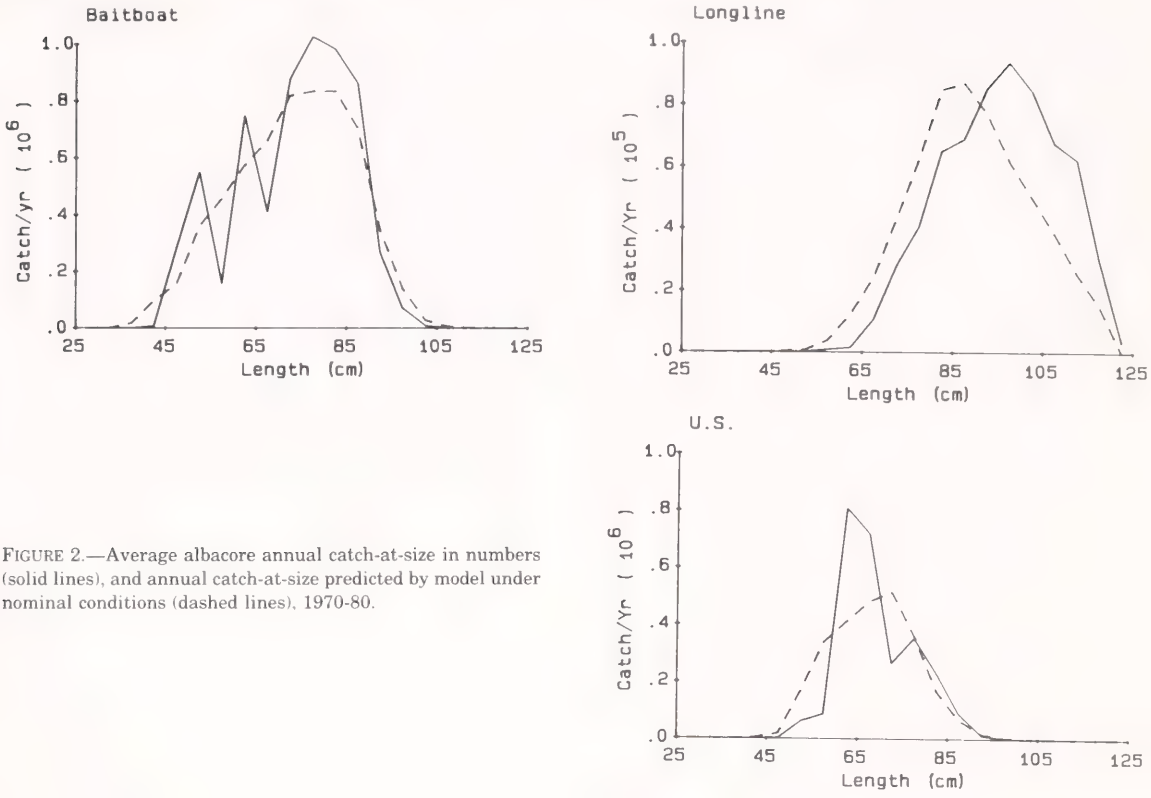

FIGURE 2.—Average albacore annual catch-at-size in numbers (solid lines), and annual catch-at-size predicted by model under nominal conditions (dashed lines), 1970-80.

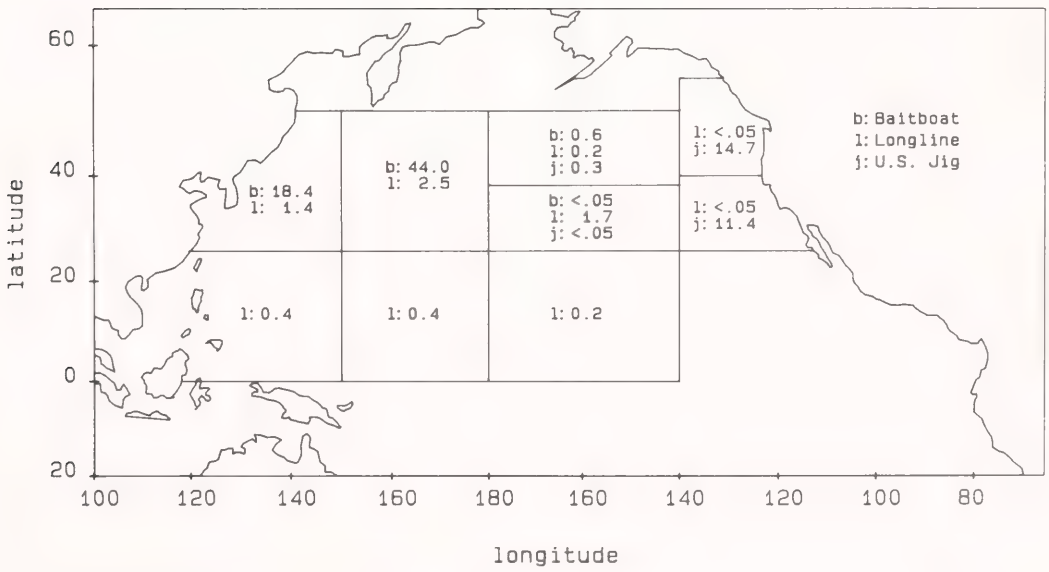

FIGURE 3.—Model zones with average annual albacore catch (numbers × 10^5) by gear type, 1970-80.

major fleets span the years 1970 through 1980. We processed the data into an "average year", that is, the average (over the years 1970-80) of catch by size, zone, month, and gear and the average of effort by zone, month, and gear (Kleiber and Baker[3]). The effort values were used directly in the model and the catch and effort used to estimate other input parameters.

We estimated the 1970-80 average recruitment and preliminary catchability values by size and gear by use of a size-structured cohort analysis (Jones 1981). The catch-at-size vector necessary for this cohort analysis was obtained from the average year by aggregating over zones, averaging over months, and smoothing over size classes.

To conduct the cohort analysis, we needed to specify an average final cohort size, which was unknown to us. We tried a series of values and chose results for which the overall exploitation rate (catch divided by recruitment estimate) was close to the overall exploitation rate estimated from tagging. Tagged albacore have been released in the U.S. fishery at an average size of approximately 65 cm, and approximately 6% of the tags have been recovered (Laurs[4]). Nonreporting losses are small for the major fisheries that recovered the tags (Laurs[5]). Assuming a value of 10% for nonreporting and Type I and II tag losses of 12% and 0.098 year^{-1} respectively (Laurs et al. 1976), the exploitation rate of recruits to 65 cm should be approximately twice the raw recovery percentage. But the exploitation rate in the cohort analysis and the simulation model is based on recruits to 25 cm which should be approximately twice as numerous as recruits to 65 cm (based on growth and natural mortality rates used in the model). Therefore, the exploitation rate of recruits to 25 cm should be approximately equal to the raw tag recovery percentage (6%). We chose a cohort analysis with an exploitation rate of 6.3% as the basis for the results presented below except where we discuss sensitivity to exploitation rate for which we repeated the analysis several times starting at this point with a series of cohort analyses at a series of higher exploitation rates.

[3]Kleiber, P., and B. Baker. 1986. Development of catch and effort data base for the North Pacific albacore simulation model. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-86-26, 21 p.

[4]Laurs, R. M. 1979. Results from North Pacific albacore tagging studies. U.S. Natl. Mar. Fish. Serv., Southwest Fish. Cent., Admin. Rep. LJ-79-17, 10 p.

[5]R. M. Laurs, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. March 1987.

The cohort analysis yielded a Pacific-wide recruitment estimate. We apportioned one third of this recruitment to each of the three southern zones, where albacore larvae are predominantly found (Nishikawa et al. 1984).

Size-specific overall fishing mortalities obtained from the cohort analysis were apportioned to gear type by the proportion of the total catch at each size that is taken by each gear type in the average year. We then converted the fishing mortalities into catchabilities by dividing by the overall average effort for each gear type.

Size-specific growth coefficients, G_s, were the growth rates in length (dl/dt) at the upper end of each size class divided by the length of the size classes (5 cm). We estimated the growth rates from the derivative form of the von Bertalanffy growth equation

$$\frac{dl}{dt} = k(l_\infty - 1)$$

where l_∞ is 135.6 cm and k is 0.014 month^{-1} (Clemens 1961). We used these same values in the size-structured cohort analysis, which required input of growth information.

A value for natural mortality was also needed both in the cohort analyses and in the model. We used a value of 0.017 month^{-1} (0.2 year^{-1}) (Suda 1966).

The tag data would be a good source of information to estimate migration coefficients except that the tag recovery effort is not uniformly distributed and analytical techniques to deal with that situation are not well developed. To get a reasonable set of migration coefficients, we quantified the experience of three experts, scientists knowledgeable about the North Pacific albacore fisheries and the available tag data. We first asked the experts to identify the significant paths (movement from one zone to an adjacent zone) for each of a series of broad (10 cm) size classes. For each path we then asked how the intensity of migration via that path is distributed over the months of the year and we evaluated the average intensity by asking the experts the following question: On average, during the season of this migration, if 100 fish of the given size class are now in the origin zone, how many of these (irrespective of mortality) would be expected to be in the destination zone one month from now? We calculated the average migration coefficient for the particular path by

$$\bar{\mu} = \ln\left[\frac{100}{100 - X}\right]$$

where X is the answer to the above question. The monthly migration coefficients were then obtained by scaling the distribution of intensity over months so that the average was equal to $\bar{\mu}$. The migration coefficients for the 10 cm size classes were then assigned to the smaller (5 cm) size classes used in the model, and the coefficients smoothed over size to soften discontinuities.

The pattern of movement represented by the migration coefficients can be summarized as follows: For immature fish (<85 cm) in the zones north of 25° north the pattern is vigorous seasonal movement toward the east in the summer and toward the west at other times. New recruits, which appear in the southern zones, migrate mainly northward throughout the year and are entrained in the east-west excursions of the northern zones. Mature fish (>85 cm) accumulate in the southern zones with brief movements northward in April and May.

RESULTS

When we ran the model with input values estimated as described above and with the effort of all fleets set at nominal levels, that is, the average seasonal and geographic pattern and magnitude of effort for the 1970s with the pattern repeated year after year, we found that after 10 years of simulation the seasonal and geographic pattern and magnitude of catch closely repeated itself year after year. Therefore in making comparisons of model results under different conditions, we allowed the model to run at least 10 years under a given repetitive annual regime before recording the catch results during 1 year of simulation.

In using the preliminary catchability values in the model, we found that the predicted catches were too low and the exploitation rate achieved (2.6%) was less than half the exploitation rate in the cohort analysis, which estimated those catchability values (6.3%). This is because the cohort analysis could not deal with geographic and seasonal variability. The fleets were presumed to be harvesting the ocean-wide population rather than the fish in a localized area and time as in the simulation model. We therefore scaled the catchabilities of each fleet upward to make the annual catches in number in the model (after 10 years of simulation) close to the real average annual catches (Kleiber and Baker fn. 2). With the corrected catchabilities, an exploitation rate of 5.1% was achieved and we took the results in this case to be our nominal (control) results (Fig. 2, Table 1).

We then made runs in which the original seasonal and geographic pattern of effort was maintained but the magnitude of effort of one of the fleets was either doubled or halved. We could then compare the annual catch of each fleet under the changed (experimental) conditions with the annual catch under nominal conditions.

TABLE 1.—Average albacore annual (1970-80) catch in numbers and metric kilotons (kt) by baitboat, longline, and U.S. fleets plus annual catch from model after at least 10 years of simulation under nominal conditions and under various conditions of altered fishing effort.

		baitboat		longline		U.S.	
		number (10^6)	kt	number (10^6)	kt	number (10^6)	kt
average catch		6.29	57.52	0.68	13.30	2.65	19.56
nominal effort		6.87	55.12	0.66	9.47	2.67	18.32
baitboat effort	× 2	12.89	102.00	0.62	8.76	2.63	18.05
	÷ 2	3.55	28.69	0.69	9.86	2.69	18.46
longline effort	× 2	6.85	54.91	1.32	18.79	2.67	18.30
	÷ 2	6.88	55.23	0.33	4.75	2.67	18.33
U.S. effort	× 2	6.80	54.43	0.65	9.23	5.19	35.41
	÷ 2	6.90	55.49	0.67	9.59	1.35	9.32

The catch-at-size for the three fleets under nominal and experimental conditions is plotted in Figures 4 to 6. Changes in effort in one fleet appear to have little effect on the size distribution in the catch of any of the fleets.

The effect on amount caught is another matter. Total catch of all sizes, both in numbers and in weight, is given in Table 1. We obtained catch in weight by converting the number caught in each length category to weight using the length-weight relationship of Clemens (1961) and then by summing over length categories. The effects are summarized in Tables 2 and 3 where the change from nominal catch for each fleet is given for each experimental treatment. By far the largest effect of a change in effort of any fleet is the effect on its own catch. A doubling of the baitboat effort causes the largest between-fleet effect, which is a 7.5% depression of the longline catch in weight, a loss of approximately 700 t (Table 3). A similar loss to the baitboat fleet, due to doubling of U.S. effort, is only a 1.3% decrease in the baitboat catch (Table 3).

We tested the sensitivity of our results to the

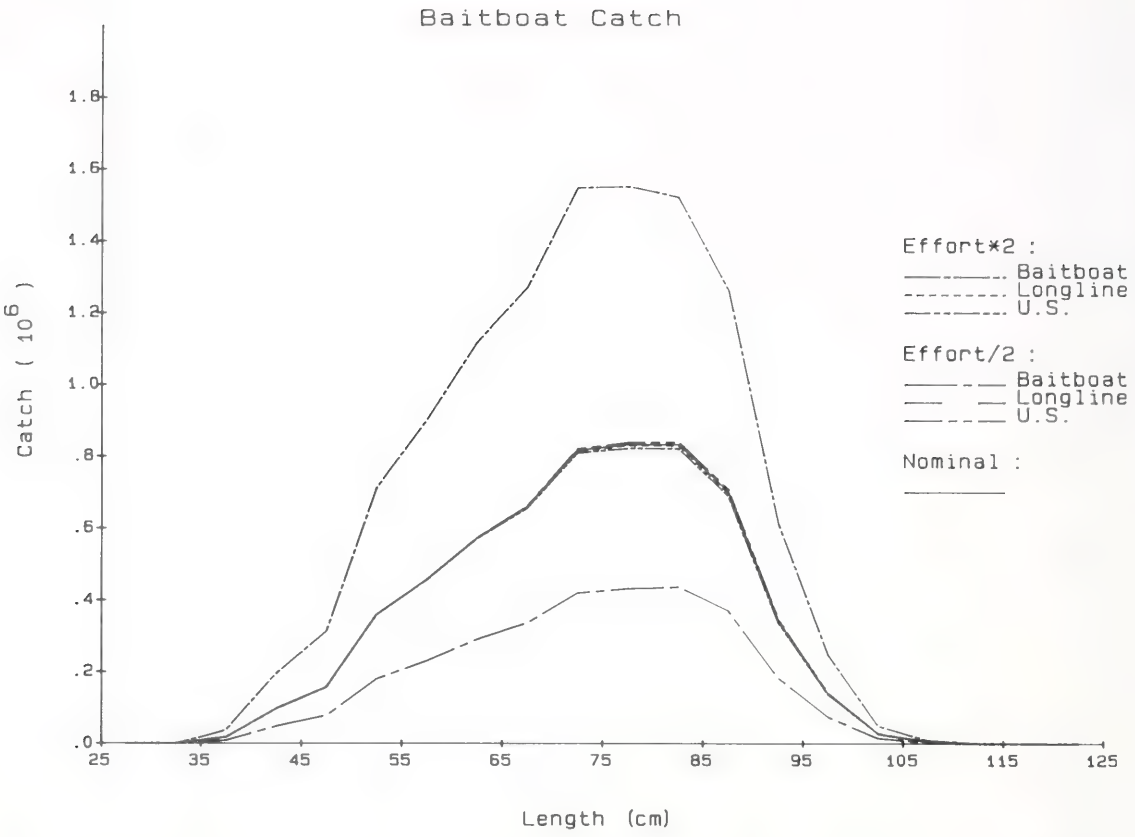

FIGURE 4.—Annual albacore baitboat catch-at-size in numbers predicted by the model under nominal and experimental conditions.

TABLE 2.—Interaction matrix for annual albacore catch in numbers. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇩ / effect ⇒		Δ catch: number × 10^6 (%)					
		baitboat		longline		U.S.	
baitboat	× 2	6.02	(87.6)	−0.04	(6.1)	−0.04	(1.5)
effort	÷ 2	−3.32	(48.3)	0.03	(4.5)	0.02	(0.7)
longline	× 2	−0.02	(0.3)	0.66	(100.0)	0.00	(0.0)
effort	÷ 2	0.01	(0.1)	−0.33	(50.0)	0.00	(0.0)
U.S.	× 2	−0.07	(1.0)	−0.01	(1.5)	2.52	(94.4)
effort	÷ 2	0.03	(0.4)	0.01	(1.5)	−1.32	(49.4)

TABLE 3.—Interaction matrix for annual albacore catch in weight. The values given are the differences between the catch under altered effort and the nominal catch (percent of nominal catch in parentheses).

cause ⇩ / effect ⇒		Δ catch: kt (%)					
		baitboat		longline		U.S.	
baitboat	× 2	46.88	(85.1)	−0.71	(7.5)	−0.27	(1.5)
effort	÷ 2	−26.43	(47.9)	0.39	(4.1)	0.14	(0.8)
longline	× 2	−0.21	(0.4)	9.32	(98.4)	−0.02	(0.1)
effort	÷ 2	0.11	(0.2)	−4.72	(49.8)	0.01	(0.1)
U.S.	× 2	−0.69	(1.3)	−0.24	(2.5)	17.09	(93.3)
effort	÷ 2	0.37	(0.7)	0.12	(1.3)	−9.00	(49.1)

overall exploitation rate by repeating the whole analysis at higher exploitation rates, starting with the cohort analysis, correcting catchabilities to give a new set of nominal results, and finally measuring the most sensitive interaction, the effect of doubled baitboat effort on the longline catch (Fig. 7). The degree of interaction is not affected very much when the exploitation rate is below 10%, but it rises quickly at higher exploitation rates.

DISCUSSION

Our results support the notion that fishery interaction is not of great consequence, at least for the North Pacific albacore fisheries typical of the

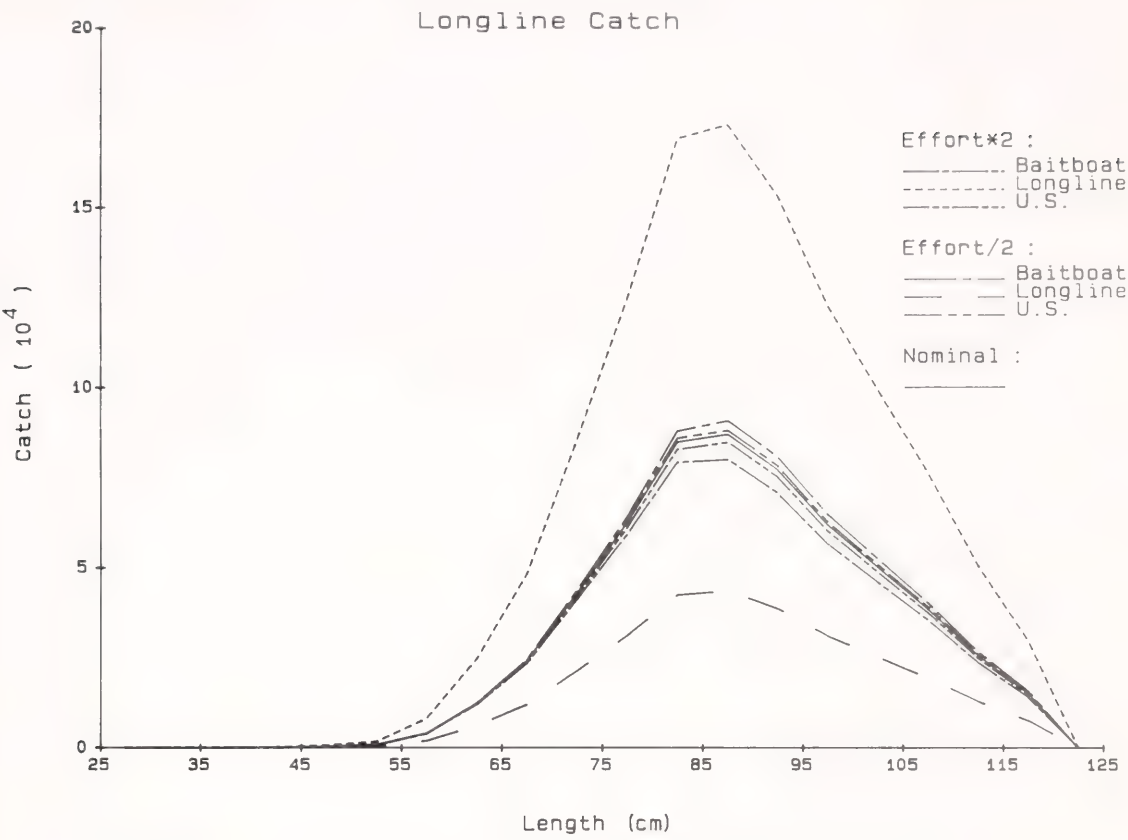

FIGURE 5.—Annual albacore longline catch-at-size in numbers predicted by the model under nominal and experimental conditions.

1970s. The reliability of this conclusion, of course, depends on the reliability of our simulation model, but in evaluating the behavior of the model, we should remember that what is important is the response of the model to experimental manipulation not the exactitude of the nominal behavior in comparison to real data. Of course, if the nominal behavior is outlandish, the responses to manipulation will be suspect. Therefore we used the average year as a signpost to tune the nominal results of the model into the range of plausible behavior, but we did not insist on exact duplication of the average year (itself an abstraction that never happened in reality).

A case in point is the longline catch, which under nominal conditions in the model is less (in weight) than any of the real annual longline catches for the years 1970-80. The average over those years is 13.3 metric kilotons (kt) per year whereas the nominal longline catch in the model is 9.47 kt/year (Table 1). The discrepancy is explained by the fact that the average size of fish in the model longline catch is less than the average size in the real longline catch, because large fish in the model migrate out of reach of the longline fleet more than they should. We have not corrected this problem because we are waiting for further information from tagging studies to get better estimates of migration coefficients. We expect the corrections to be quantitative refinements of the existing values and not a qualitative change in the current migration pattern in the model.

What is important in the current context is that bias in the nominal results is bound to show up in the experimental results as well. The migration coefficients were the same in both control and experimental situations in the model. Therefore, refinements to the coefficients are not likely to make much difference in the relative values in Tables 2 and 3, particularly in the percentages. It is pertinent that our conclusion of low interaction

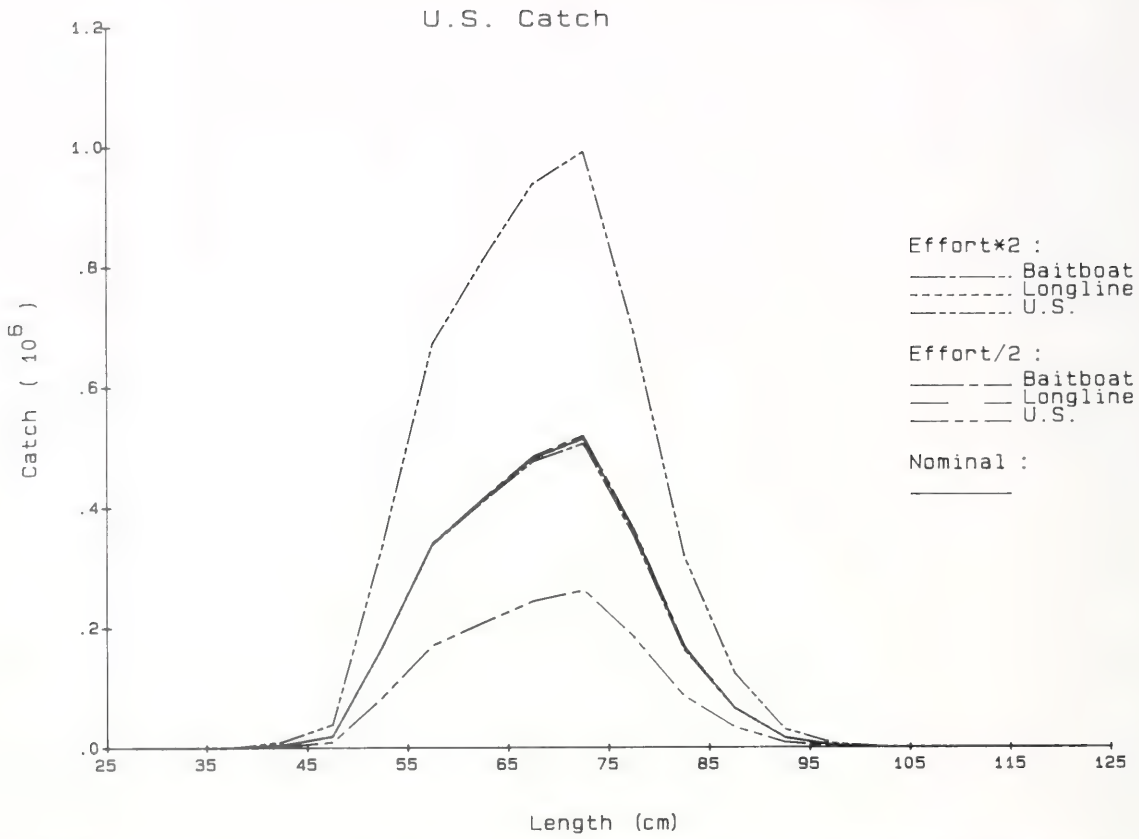

FIGURE 6.—Annual albacore U.S. catch-at-size in numbers predicted by the model under nominal and experimental conditions.

(expressed as percent) persisted through a series of updates of the model (such as changes in configuration of geographic strata) and inevitable updates and corrections of the fishery data base.

Though the nominal behavior of the model need not conform precisely to the mean behavior of albacore fisheries in the 1970s (however that might be defined), the behavior should, nonetheless, be a plausible representation of the albacore fisheries in that period. We have seen, for example, that our conclusion would be suspect if the actual exploitation rate were considerably higher than the 6% value that we assumed (Fig. 7), but such high exploitation levels would be contrary to the tag return results.

We have only tested the effects of changes in the magnitude of effort, not changes in seasonal and geographic pattern of effort, which might cause the fleets to overlap much more than they do. However, our experimental treatment of doubling the effort of a fleet is tantamount to adding

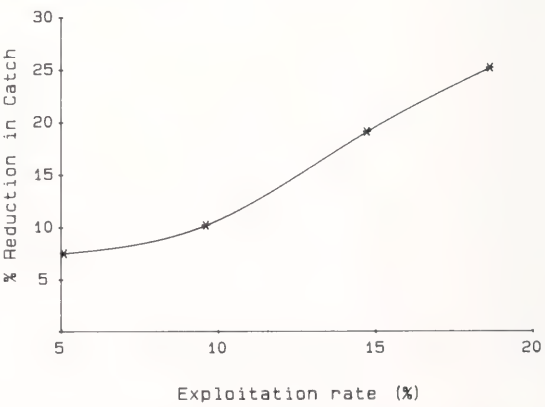

FIGURE 7.—Sensitivity of interaction to overall exploitation rate. The ordinate is the percent reduction from nominal levels in annual albacore longline catch in weight as a result of doubling the baitboat effort.

a completely overlapping, competing fleet. The response of each fleet to doubling of its own effort was close to a 100% increase in catch (Tables 2, 3), indicating that the degree of competition was low. Therefore, it would be difficult to design a realistic experimental treatment that 1) would be simply a shift in the geographic and seasonal pattern of effort in one fleet (not a change in magnitude), and 2) would have a strong impact on another fleet.

A legitimate question is whether our conclusions, which are based on 1970s data, can be extrapolated to the current conditions. The most striking change in recent years is the emergence of the gill net fishery for albacore, which now takes approximately 20% of the total catch. However, because the total catch has not increased, the exploitation rate must still be mild, and we would expect that interaction between fleets would also still be mild. We cannot use our model to estimate interaction quantitatively in this situation because we lack detailed data on the gill net fishery.

CONCLUSIONS

The implication of our results is that fleet interaction is not likely to be significant if the pattern and magnitude of effort in the 1970s are maintained. This assessment could change if the overall exploitation rate increases considerably. The recent emergence of the gill net fishery could be of significance in this regard. The levels of annual catch that have been reported by this fishery are not likely to be of concern, but the significance cannot be confidently evaluated unless detailed catch, effort, and size distribution data are made available.

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AGE DETERMINATION OF PACIFIC COD, *GADUS MACROCEPHALUS*, USING FIVE AGEING METHODS[1]

HAN-LIN LAI,[2] DONALD R. GUNDERSON,[3] AND LOH LEE LOW[4]

ABSTRACT

A comparative study of age determination methods for Pacific cod, *Gadus macrocephalus*, was carried out using dorsal and pectoral fin rays, scales, otoliths, and coracoids. A preliminary validation using the modal length of a strong year class confirmed that sections of dorsal fin rays were the most reliable ageing method. A Monte Carlo method was developed for converting scale ages to dorsal fin-ray ages. An analysis by log-linear model was developed for testing the effects of ageing method and age class on repeatability of age reading.

Scales have been widely used for ageing Pacific cod, *Gadus macrocephalus*, in the North Pacific since Kennedy (1970) developed the method for fish in Hecate Strait, British Columbia. However, Bakkala (1981)[5] found that the scale method may not be an appropriate ageing method since the estimated ages from scales do not appropriately reflect the progress of known year classes in the eastern Bering Sea. Beamish et al. (1978) also found that Kennedy's criteria might not be satisfactory for scales from juvenile Pacific cod in Canadian waters.

Beamish (1981) reported that thin sections of fin rays can be reliably aged and might be more accurate than scale ages when ageing older fish. However, Westrheim and Shaw (1982) encountered difficulties with fin-ray cross sections and reported that fin-ray ages were younger than scale ages. They also discovered false checks on the scales during the first year of life, which fitted the annulus criteria of Kennedy (1970), and validated the scale ageing method for age-1 and -2 Pacific cod. Chilton and Beamish (1982) noted problems associated with scales and fin rays, and recommended a judicious mixture of scale ages, fin-ray ages and length-frequency analysis for ageing Pacific cod in Canadian waters.

In earlier studies, Mosher (1954), Moiseev (1953), and Ketchen (1970) reported that the otolith surface ageing method was not satisfactory for Pacific cod. Ketchen (1970) also had no success with ageing of vertebrae, or opercula. Lai (1985) reported that age determination from the bony tissues in the gillcover, scapula, and cleithrum was not feasible.

This paper reports the results of a comparative study and preliminary validation of age determination methods for Pacific cod in the eastern Bering Sea using dorsal and pectoral fin rays, scales, otoliths and coracoids. In addition, we develop a method to convert scale ages to dorsal fin-ray ages. This age conversion method makes it possible to use existing ages estimated from scales.

MATERIALS AND METHODS

Dorsal and pectoral fin rays, otoliths, and scales were taken from 230 Pacific cod collected from foreign fishing vessels operating in the eastern Bering Sea during September 1983 to March 1984. Among these samples, coracoids were also taken from 101 fish.

Dorsal and pectoral fin-ray sections were prepared using an Isomet low-speed saw (Lai 1985), and the annuli were identified by the criteria of Beamish (1981) and Chilton and Beamish (1982). Scale images were made by acetate plate (Koo 1962) and then read by a microfisch reader. Annuli on scales were identified by the methods de-

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scribed in Westrheim and Shaw (1982). Otoliths must be sectioned with a low-speed electric saw and burnt with care, as they are quite brittle. The interpretation of annuli on break-and-burn surfaces was adapted from that of walleye pollock (Lai and Yeh 1986).

The coracoid is a dermal bone connected to the scapula and radii in the pectoral girdle. A triangular component within the coracoid (Fig. 1) shows alternate opaque (dark) and translucent (light) zones under a binocular microscope and transmitted light, by which annuli can be identified. The center of this structure occasionally contains some checks that are parallel to the annulus; however, their spacing is narrower than that of regular annuli. The age samples were read

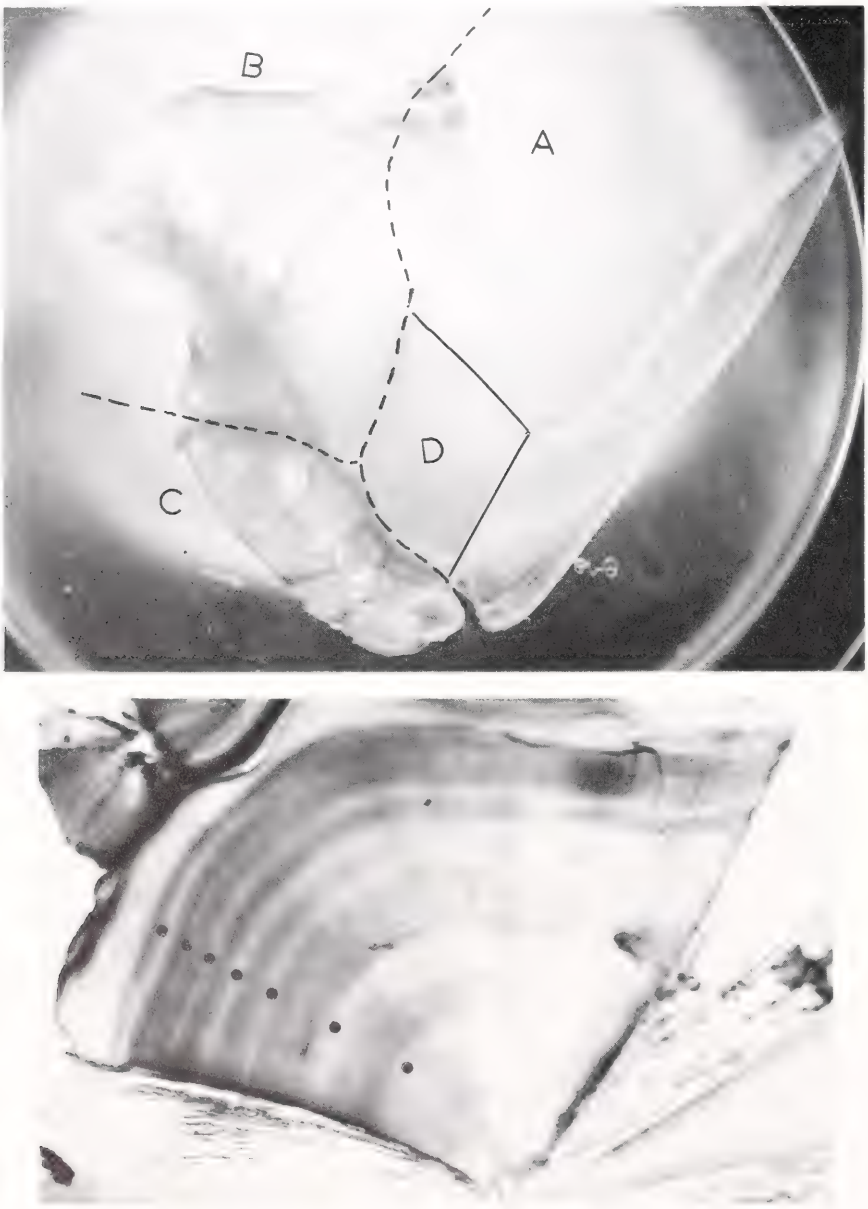

FIGURE 1.—Upper: The pectoral girdle. A, coracoid; B, scalpula; C, radii; D, the portion used for age determination. Lower: Enlarged Part D. •, translucent zone, counted as an annulus.

twice by the senior author, who had 3 years experience in age determination using all of the ageing methods.

A loglinear model (Fienberg 1981) was used to test the independence of repeatability ($R, k = 1, 2$ corresponding to agreement and disagreement) of age readings corresponding to age-class (A, $j = 1,...,8$ corresponding to age classes given in Table 1) and ageing method (M, $i = 1,...,5$ corresponding to ageing methods in the sequence given in Table 1). See Appendix A for the details of this statistical method. The computer program P4F in BMDP (Dixon 1983) was used for computation and analysis.

TABLE 1.—Observed frequency of agreement between two age readings using different ageing methods. Percent agreement is shown in parentheses.

Method (M)	Age (A)	Repeatability (R)		
		Agree	Disagree	Total
Coracoid	under 2	9 (100)	0	9
	3	1 (50)	1	2
	4	10 (77)	3	13
	5	12 (60)	8	20
	6	18 (67)	9	27
	7	5 (45)	6	11
	8	3 (43)	4	7
	over 9	4 (40)	6	10
Total		62 (63)	37	99
Break-and-burn	under 2	9 (90)	1	10
	3	7 (64)	4	11
	4	8 (73)	3	11
	5	41 (67)	20	61
	6	35 (58)	25	60
	7	14 (39)	22	36
	8	6 (35)	11	17
	over 9	9 (41)	13	22
Total		129 (57)	99	228
Dorsal fin ray	under 2	9 (100)	0	9
	3	2 (67)	1	3
	4	13 (81)	3	16
	5	36 (77)	11	47
	6	40 (82)	9	49
	7	24 (69)	11	35
	8	9 (39)	14	23
	over 9	7 (29)	17	24
Total		140 (68)	66	206
Pectoral fin ray	under 2	8 (100)	0	8
	3	6 (75)	2	8
	4	18 (64)	10	28
	5	36 (68)	17	53
	6	24 (45)	29	53
	7	12 (43)	16	28
	8	10 (45)	12	22
	over 9	3 (25)	9	12
Total		117 (55)	95	212
Scale	under 2	9 (82)	2	11
	3	11 (61)	7	18
	4	60 (74)	21	81
	5	48 (64)	27	75
	6	11 (38)	18	29
	7	1 (11)	8	9
	8	0 (0)	1	1
	over 9	0 (0)	1	1
Total		140 (62)	85	225

An analysis of variance (ANOVA) model with repeated measures (Winer 1971) was used to examine variability in age readings due to the methods. The ANOVA model was

$$X_{ijn} = \mu + \pi_n + M_i + (M\pi)_{in} + R_j + (R\pi)_{jn} + (MR\pi)_{ijn} + \epsilon_{ijn}$$

where, X_{ijn} is the observed age of the nth fish by the ith ageing method and jth reading,

$i = 1, 2, 3, 4, 5$ indicates ageing methods in the sequence shown in Table 1,

$j = 1, 2$ indicates the first and second age readings,

$n = 1,...,N$ indicates number of fish,

μ is the grand mean,

π is the effect between subjects (individual fish),

M is the effect of ageing method,

R is the effect of reading,

$(M\pi)$, $(R\pi)$, and $(MR\pi)$ are the two- and three-factor interactions of effects M, R, and π, and

ϵ is the random error.

Readings from coracoids were not included in the analysis because of the small sample size. Specimens with missing values were also excluded from this analysis. The Q-statistic (Snedecor and Cochran 1967) was used to test the differences between the mean ages between readings and between ageing methods.

Validation of age determination was carried out by comparing the mean lengths at age estimated from the five ageing methods to the modal lengths of the 1977 year class. The progression of this year class could be traced by examining the length-frequency distributions for 1978 to 1983.

Because existing age data files for Pacific cod at the Northwest and Alaska Fisheries Center (NWAFC) were derived from scales, it is important to explore whether or not the scale age data can be used for stock assessment. A simulation study was carried out to convert a scale age-length key to a dorsal fin-ray age-length key,

since the dorsal fin-ray method provides more accurate ages.

Age-length keys, derived from scales collected in 1979 and 1980 NWAFC demersal trawl surveys in the eastern Bering Sea, and length-frequency distributions obtained from these surveys were used as basic data to be converted. The classification probabilities for fin rays vs. scales were constructed from 966 age readings on dorsal fin rays and scales from the same fish collected in 1983-84 (Table 2). Each fish in the 1979 and 1980 scale age-length key was assigned a "pseudo" dorsal fin-ray age, which was a random variate generated from the subprogram GGDA in IMSL (International Mathematical and Statistical Library). The GGDA subroutine used the prior probability density in Table 2 corresponding to the scale age and length group to which the fish belongs. This was done 30 times to create 30 converted age-length keys each for 1979 and 1980. Then, mean lengths at age were determined from each converted age-length key, and age compositions were estimated by the method described in Lai (1987). These simulated results were compared with those from length-frequency analysis (Lai 1985).

RESULTS

Table 1 shows that the age readings from dorsal fin rays had the highest percent agreement (68%), followed by coracoids (63%), scales (62%), otoliths (57%), and pectoral fin rays (55%). Furthermore, the percent agreement for the major age classes in the fishery (ages 4-7) were much higher than for the other methods. To confirm this result, a log-linear model was fitted to the data in Table 1.

Table 3 shows that the best log-linear model (Appendix A) was

$$\theta_{ijk} = \log(m_{ijk}) = \mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} \quad (2)$$

TABLE 2.—Observed classification probability for age readings from scales and dorsal fin-rays.

Scale age	Length (cm)	Dorsal fin-ray age														
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
1	20-29	1.0														20
1	30-39		1.0													6
2	30-39		1.0													8
2	40-49			0.750	0.250											8
3	30-39		1.0													2
3	40-49			0.333	0.667											3
3	50-59				0.188	0.375	0.375	0.063								32
3	60-69				0.087	0.565	0.174	0.130	0.043							23
4	40-49				0.133	0.467	0.400									15
4	50-59				0.604	0.264	0.094	0.038								53
4	60-69				0.066	0.377	0.221	0.197	0.098	0.041						122
4	70-79					0.153	0.350	0.190	0.065	0.058	0.066	0.051	0.036	0.029		137
4	80-89						0.348	0.217	0.174	0.130	0.043	0.087				23
5	50-59				0.143	0.857										14
5	60-69				0.043	0.391	0.239	0.196	0.109	0.022						92
5	70-79				0.005	0.095	0.264	0.206	0.180	0.116	0.069	0.048	0.016			189
5	80-89						0.154	0.128	0.205	0.256	0.154	0.077	0.026			39
5	90-99										0.500	0.500				2
6	60-69							0.611	0.222	0.167						18
6	70-79				0.017	0.083	0.333	0.233	0.167	0.117	0.033	0.017				60
6	80-89						0.188	0.344	0.156	0.125	0.125	0.063				32
6	90-99							0.059	0.412	0.176	0.118	0.118	0.118			17
6	100-109										0.500	0.500				4
7	70-79						0.333	0.111	0.333	0.111					0.111	9
7	80-89						0.182			0.545		0.182		0.090		11
7	90-99							0.063	0.187	0.250	0.187	0.063	0.250			16
8	80-89									0.400	0.200	0.400				5
8	90-99									0.333		0.167	0.333	0.167		6

TABLE 3.—Test for the independence of percent agreement (R) of age readings correlated to age-class (A) and ageing method (M).

Model	df	G^2	Probability
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} + \lambda_{ijk}^{MAR}$	0	0.00	1.0000
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA}$	28	28.08	0.4603
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR}$	32	48.87	0.0285
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{jk}^{AR} + \lambda_{ij}^{MA}$	56	241.75	0.0000
$\mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{ij}^{MA}$	35	125.03	0.0000

which implied that percent agreement was correlated to age-class and ageing method, and the estimated age frequencies differed by ageing method. However, these pairwise relationships between any two factors are unrelated to the third.

Because we are interested in the effects of ageing method and age class on repeatability, it is reasonable to look at the ratio between agreement ($k = 1$) and disagreement ($k = 2$) for each combination of ageing method and age class, i.e., m_{ij1}/m_{ij2} for all i and j. The logarithm of this ratio is known as the logit model (Fienberg 1981, chapter 6). The logit model for Equation (2) can be derived as

$$\text{logit}(i,j) = \log\,(m_{ij1}/m_{ij2}) = \omega + \omega_i^M + \omega_j^A \qquad (3)$$

where, the logit effects, $\omega = (\lambda_1^R - \lambda_2^R)$, $\omega_i^M = (\lambda_{i1}^{MR} - \lambda_{i2}^{MR})$, and $\omega_j^A = (\lambda_{j1}^{AR} - \lambda_{j2}^{AR})$. The effects ($\lambda$'s) without factor R in Equation (2) are cancelled out by subtraction in Equation (3). The values of λ's can be obtained from the BMDP program and substituted into Equation (3). The results show that there was a significant declining effect on agreement as age increased (Table 4). This indicated that percent agreement decreased with increasing age. Age determination using coracoids and dorsal fin rays had a positive effect on agreement, which indicated that agreement of these methods was higher than the average of the five methods, but the other ageing methods had a negative effect, i.e., agreement was lower than average.

Table 5 shows that the effect of ageing method was significant for all fish older than age 3. There was no significant difference (5% level) between readings except for ages 5-6. This difference probably resulted from differences between readings for otoliths and pectoral fin rays (Table 6). Mean square (MS) for the ageing method effect increased with age and was the predominant component in the within-subject variation for all age categories. Therefore, variability in age determination was mainly due to ageing method rather than inconsistent annulus interpretation by the reader.

TABLE 4.—Estimated logit effects corresponding to the loglinear model in Equation (2).

Factor		Logit effect
constant (ω)		0.540
Age (ω_j^A)	≤2	2.204
	age 3	0.240
	age 4	0.676
	age 5	0.278
	age 6	−0.196
	age 7	−0.738
	age 8	−1.064
	over 9	−1.400
Age method (ω_i^M)	Dorsal fin ray	0.568
	Coracoid	0.096
	Otolith	−0.058
	Pectoral fin ray	−0.208
	Scale	−0.398

Using the Q-statistic, the mean ages of the two readings were not significantly different except for age group 5-6 using otolith and pectoral fin-ray ageing methods (Table 6). Significant differences between ageing methods were found in all age categories except the youngest. Age readings from dorsal fin rays and pectoral fin rays were not significantly different for fish younger than age 6. Age readings from otoliths and pectoral fin rays were not significantly different for fish older than age 7. Otolith readings were older than other methods for fish younger than age 6 but were younger than dorsal fin-ray readings for fish older than age 7. Scale readings gave consistently younger ages than the other methods.

Bakkala and Wespestad (1984) reported that recruitment of the 1977 year class was uniquely strong when compared to its neighboring year classes. The modal length of this year class can be

TABLE 5.—Comparison of ageing variability of Pacific cod by ANOVA.

Dorsal fin-ray age	N		Between subject (π)	Within subject: Method (M)	$M\pi$	Reading (R)	$R\pi$	MR	$MR\pi$
1-2	8	SS	14.359	0.297	2.578	0.016	0.109	0.047	1.328
		df	7	3	21	1	7	3	21
		MS	2.051	0.099	0.123	0.016	0.016	0.016	0.063
		F		0.81		1.00		0.25	
3-4	19	SS	52.395	8.967	38.658	0.164	3.711	0.072	7.553
		df	18	3	54	1	18	3	54
		MS	2.911	2.989	0.716	0.164	0.206	0.024	0.140
		F		4.18**		0.80		0.17	
5-6	93	SS	270.495	166.154	273.721	1.840	26.285	1.122	74.253
		df	92	3	276	1	92	3	276
		MS	2.940	55.385	0.992	1.840	0.286	0.374	0.269
		F		55.85**		6.44**		1.39	
7-8	57	SS	217.244	344.018	267.232	0.219	26.031	0.921	56.829
		df	56	3	168	1	56	3	168
		MS	3.879	114.673	1.591	0.219	0.465	0.307	0.338
		F		72.09**		0.47		0.91	
9+	23	SS	339.457	498.283	198.717	0.035	21.652	1.869	53.130
		df	22	3	66	1	22	3	66
		MS	15.430	166.090	3.011	0.348	0.984	0.623	0.805
		F		55.16**		0.35		0.77	

** = significant at 1% level.

TABLE 6.—Tests for differences between mean ages of Pacific cod using various ageing methods. Bracket and underline: not significantly different at 5% level.

Dorsal fin-ray age	N	Reading	Dorsal fin ray	Otolith	Pectoral fin ray	Scale	SD	df
1-2	8	1	1.375	1.375	1.375	1.250	0.063	7
		2	1.375	1.475	1.375	1.250		
		Method mean	1.375	1.425	1.375	1.250	0.124	21
3-4	19	1	3.842	4.211	3.842	3.579	0.147	18
		2	3.847	4.315	3.895	3.579		
		Method mean	3.895	4.263	3.869	3.579	0.194	54
5-6	93	1	5.505	5.774	5.430	4.581	0.078	92
		2	5.588	5.979	5.591	4.570		
		Method mean	5.547	5.877	5.511	4.576	0.103	276
7-8	57	1	7.386	6.561	6.614	5.000	0.128	56
		2	7.316	6.702	6.737	4.982		
		Method mean	7.351	6.632	6.676	4.991	0.167	168
9+	23	1	10.130	8.000	8.304	5.522	0.293	22
		2	9.913	8.261	8.130	5.304		
		Method mean	10.022	8.131	8.217	5.413	0.362	66

traced from the length-frequency distributions from 1978 to 1983 (Fig. 2). Using the method of Macdonald and Pitcher (1979), the mean lengths for ages 1-6 were 22, 35, 43, 52, 61, and 64 cm respectively (Lai 1985) and were very close to the modal length of length-frequency distributions. Figure 2 shows the mean lengths at age estimated from the 1983-84 samples by the five ageing methods and the comparison to the modal lengths. It is apparent that the mean lengths at age estimated from dorsal fin rays were closest to the modal lengths. Also, the variability around mean length at age estimated from dorsal fin rays was generally smaller than for the other methods. We also used the index of variation[6] (IV, Lai

[6] $IV = 100\% \cdot \sqrt{\Sigma(Y_i - X_i)^2/[(n-1)(\overline{X} + \overline{Y})/2]}$, where X_i is the first age reading, Y_i is the second age reading, n is the sample size, and $\overline{X}$ and $\overline{Y}$ are mean of the X_i and Y_i (Lai 1985). This indicates the degree of variation between the two

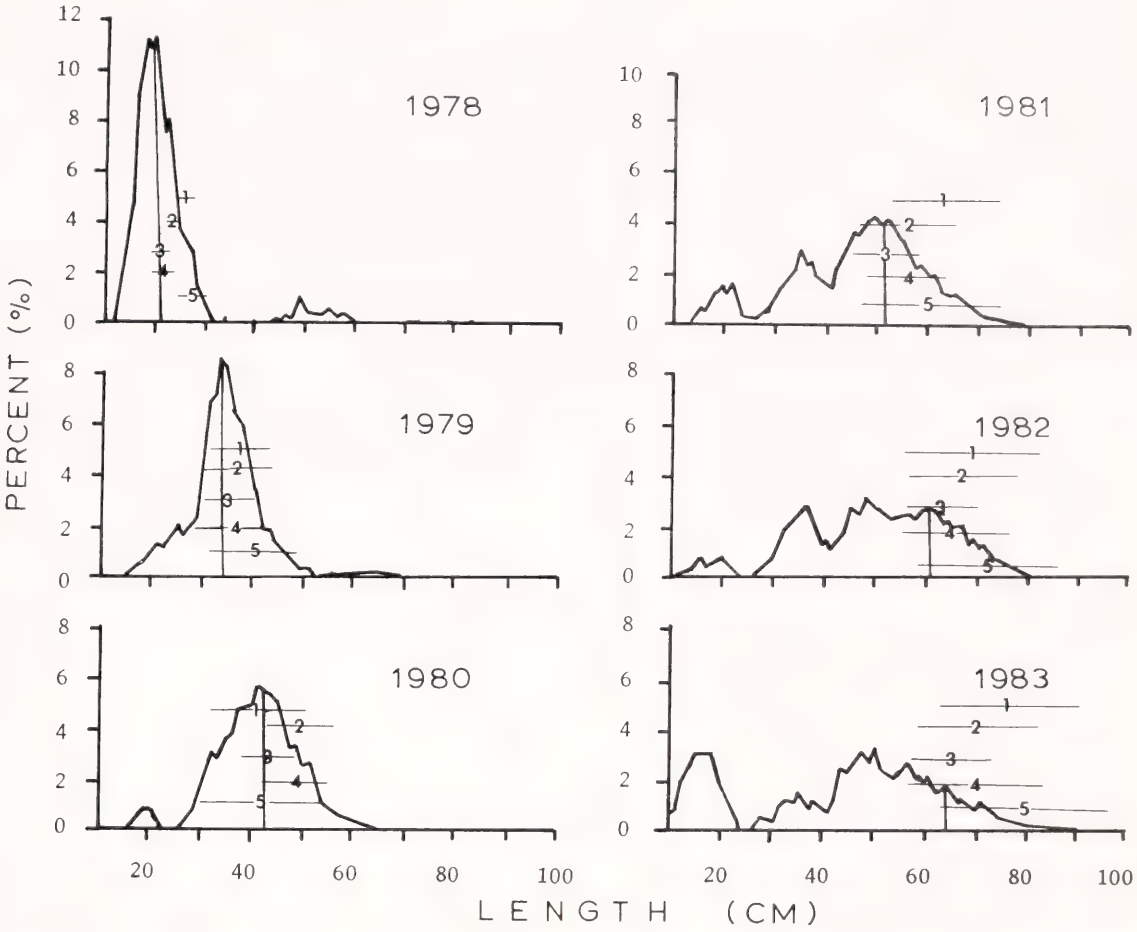

FIGURE 2.—Length-frequency distributions collected from trawl surveys in 1978-83 (after Bakkala and Wespestad 1984). The mode in 1978 represents age-1 Pacific cod of the 1977 year class, and progresses from age 2 to age 6 in the subsequent years. The estimated mean lengths at ages 1-6 estimated from the five ageing methods (1, coracoids; 2, otoliths; 3, dorsal fin rays; 4, pectoral fin rays; and 5, scales) correspond to the age of 1977 year class. Horizontal lines indicate 95% confidence interval around means. Vertical lines indicates the mean length from length-frequency analysis.

1985) to examine the degree of precision. Among the five ageing methods, the IV for dorsal fin rays was the lowest (13%) when compared with other methods (14%, 14%, 15%, and 16% respectively for otoliths, coracoids, scales, and pectoral fin rays).

The accuracy of converting scale ages to dorsal fin-ray ages was also evaluated. Mean length at age and age composition (obtained by using converted dorsal fin-ray ages) were compared with corresponding results from length-frequency analysis (Macdonald and Pitcher 1979). The 95% confidence interval (Fig. 3) for each converted mean length at age in 1979 and 1980 included the corresponding value estimated from the length-frequency analysis. However, the mean lengths at age derived from scales were significantly different from the other two.

The age composition estimated by the scale method showed a monotonic decrease with age in 1979, and the strong 1977 year class (age 2) was not evident (Fig. 4). Nevertheless, length-frequency data from surveys indicated that age-2 fish were dominant in 1979 (Bakkala and Wespestad 1984). The age composition based on converted dorsal fin-ray ages was dominated by age-2 fish and was similar to that estimated from the

ages being compared taking the age distribution of the sample into account.

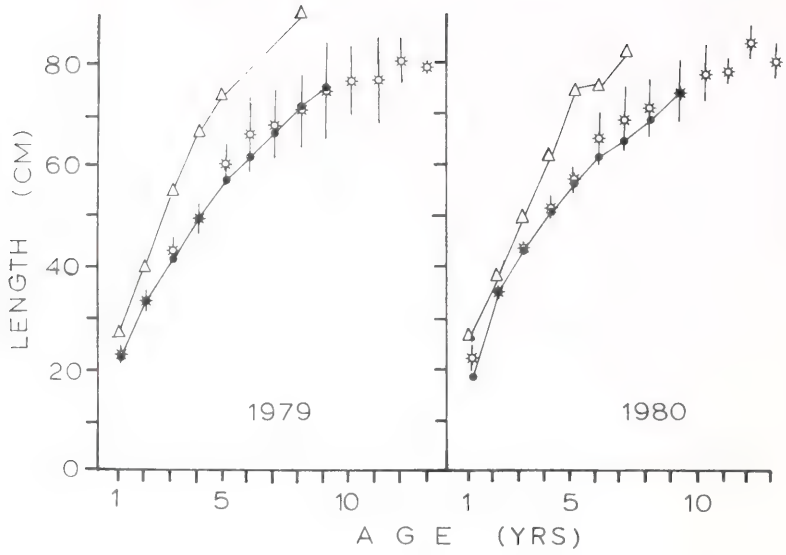

FIGURE 3.—Comparison of mean length at age estimated from scales (—Δ—), converted dorsal fin-ray ages (*), and length-frequency analysis (—●—) for 1979 and 1980. Vertical line indicates the 95% confidence interval from the 30 simulation runs.

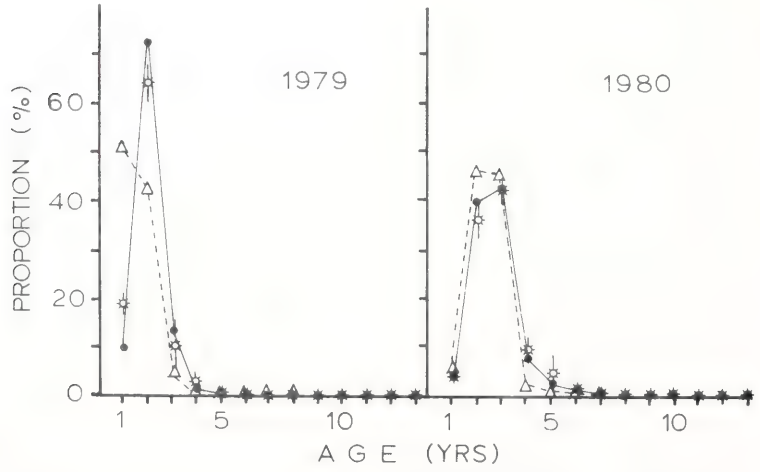

FIGURE 4.—Comparison of age composition estimated from scales (—Δ—), converted dorsal fin-ray ages (*), and length-frequency analysis (—●—). Vertical line indicates 95% confidence interval of the 30 simulation runs.

length-frequency analysis. In 1980, the proportions estimated by using the scale method were somewhat higher than for the other two methods at ages 2 and 3 (Fig. 4), but were lower at ages 4 and 5. Since the classification probabilities and scale age-length keys used in this study were derived independently from different years, the method of age conversion appears to be relatively insensitive to interannual differences in the classification probabilities.

DISCUSSION

Although Westrheim and Shaw (1982) validated the interpretation of the annuli on scales for age groups 1 and 2, this validation was not

considered to be sufficient for all age groups. Beamish et al. (1978, figs. 12 and 13) showed that the difference between readers was substantial even in age groups 1 and 2. In our study, we found that age readings from the scale method had low precision, and that scale ages were much younger than those obtained by any other method.

In this study, validation for age groups 1-6 showed that dorsal fin rays gave the most reliable ages for Pacific cod and thus should be used in the future. This method provided estimates of mean length at age that agreed most closely to observed growth of the 1977 year class, and the precision of this method was the highest attained in this study. Another major advantage of this ageing method is that additional fin rays can be taken from fish with a previous history of fin-ray removal to verify the accuracy of age determinations between time of release and recapture.

We used the Monte Carlo method to convert scale ages to dorsal fin-ray ages. The results indicated that the previously collected scale age data can be used in age-dependent methods of stock assessment. Since the 1983-84 classification probabilities used in this study were completely independent of the 1979-80 scale age data, the method appears to be robust with respect to interannual variability in the classification probabilities for Pacific cod. However, application of this method to other species will require caution when the classification probabilities are applied to the data from different years, since interannual variability could be a source of error. Still, any errors that arise will probably be smaller than those produced from an inappropriate ageing method.

Analytical methods, such as those of Pella and Robertson (1979) and Cook (1982), could also be used for converting scale age-length keys to dorsal fin-ray age-length keys. However, these methods are mathematically more complicated and occasionally yield negative values in some of the converted age-length keys (Cook 1982). The method of Hoenig and Heisey (1987)[7] is of particular interest because it avoids negative values by applying an incomplete E-M (estimation and maximization) algorithm to fit a log-linear model to the classification matrix. Nevertheless, this method may not be valid if there is a substantial systematic ageing error (as in our case, dorsal fin-ray ages vs. scale ages) because too many empty cells are in the classification matrix. Alternatively, the method of Barlow (1984) can also be used for this purpose, although the result will be very similar to our Monte Carlo method, as Barlow's method is a deterministic version of our own.

[7]Hoenig, J. M., and D. M. Heisey, 1987. Using log-linear models with the EM algorithm to correct estimates of stock composition and convert to age. Manuscr. in prep. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL.

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APPENDIX A.—ANALYSIS BY LOG-LINEAR MODEL

In our study, there are three factors, ageing method (M), age class (A), and repeatability (R). Our sampling model is product-multinomial, using the terminology of Fienberg (1981, Sec. 3-2), since the number of fish being aged is fixed for each ageing method after deleting unreadable or damaged age-structures. The aged fish were cross-classified into corresponding cells denoted by factors A and R (Table 1).

Let y_{ijk} be the observed cell frequency for the ith ageing method, the jth row of age class, and the kth column of repeatability, and let m_{ijk} be the expected value of y_{ijk}. The general log-linear model (called the saturated model because it includes the highest three-factor interaction) for our three-way ($5 \times 8 \times 2$) contingency table is

$$\theta_{ijk} = \log(m_{ijk}) = \mu + \lambda_i^M + \lambda_j^A + \lambda_k^R + \lambda_{ik}^{MR} + \lambda_{jk}^{AR} + \lambda_{ij}^{MA} + \lambda_{ijk}^{MAR} \tag{A.1}$$

where, as in the usual analysis of variance model, all effects sum up to zero over any subscript. Let $\bar{\theta}$ be the marginal mean of θ_{ijk} over the subscript which is replaced by "+" to indicate averaging, then the parameters in (Equation A.1) can be written as

$$\begin{aligned}
\mu &= \bar{\theta}_{+++} & \lambda_{ij}^{MA} &= \bar{\theta}_{ij+} - \bar{\theta}_{i++} - \bar{\theta}_{+j+} + \bar{\theta}_{+++} \\
\lambda_i^M &= \bar{\theta}_{i++} - \bar{\theta}_{+++} & \lambda_{ik}^{MR} &= \bar{\theta}_{i+k} - \bar{\theta}_{i++} - \bar{\theta}_{++k} + \bar{\theta}_{+++} \\
\lambda_j^A &= \bar{\theta}_{+j+} - \bar{\theta}_{+++} & \lambda_{jk}^{AR} &= \bar{\theta}_{+jk} - \bar{\theta}_{+j+} - \bar{\theta}_{++k} + \bar{\theta}_{+++} \\
\lambda_k^R &= \bar{\theta}_{++k} - \bar{\theta}_{+++} & \lambda_{ijk}^{MAR} &= \bar{\theta}_{ijk} - \bar{\theta}_{ij+} - \bar{\theta}_{i+k} + \bar{\theta}_{i++} \\
& & & \quad - \bar{\theta}_{+jk} + \bar{\theta}_{+j+} + \bar{\theta}_{++k} - \bar{\theta}_{+++}.
\end{aligned} \tag{A.2}$$

Log-linear models are "hierachical", i.e., higher-order interaction terms can be included only if related lower-order terms are included. For example, λ^{MAR} is not included unless λ^{AR}, λ^{MR}, and λ^{MA} are all included.

Once all expected cell frequencies (m'_{ijk}) are estimated, the goodness-of-fit for the selected model can be tested using the likelihood ratio test statistic

$$G^2 = 2 \sum_i \sum_j \sum_k y_{ijk} \log \left(\frac{y_{ijk}}{m'_{ijk}} \right) \tag{A.3}$$

which has approximately a χ^2 distribution with degrees of freedom (df) = number of cells − number of parameters (Fienberg 1981, sec. 3-3 and 3-4).

Using the partition property of G^2, we can decide whether an effect or an interaction should be included. In Table 3, for example, H_0: $\lambda^{MAR} = 0$ can be tested by examining $G^2 = 28.08 - 0.00 = 28.08$. This is not significant at the 1% level (referred to a χ^2 distribution with df = 28). Similarly, $G^2 = 20.79$ for H_0: $\lambda^{MA} = 0$, which exceeds the upper 1% tail value of a χ^2 distribution with df = 4, and is rejected. This means that λ^{MAR} will not be included in the model but λ^{MA} will. Hence, our best log-linear model is Equation (2).

SIDESCAN SONAR AS A TOOL FOR DETECTION OF DEMERSAL FISH HABITATS

K. W. Able,[1] D. C. Twichell,[2] C. B. Grimes,[3] and R. S. Jones[4]

ABSTRACT

Sidescan sonar can be an effective tool for the determination of the habitat distribution of commercially important species. This technique has the advantage of rapidly mapping large areas of the seafloor. Sidescan images (sonographs) may also help to identify appropriate fishing gears for different types of seafloor or areas to be avoided with certain types of gears. During the early stages of exploration, verification of sidescan sonar sonographs is critical to successful identification of important habitat types. Tilefishes (*Lopholatilus* and *Caulolatilus*) are especially good target species because they construct large burrows in the seafloor or live around boulders, both of which are easily detectable on sonographs. In some special circumstances the estimates of tilefish burrow densities from sonographs can be used to estimate standing stock. In many localities the burrow and boulder habitats of tilefish are shared with other commercially important species such as American lobsters, *Homarus americanus;* cusk, *Brosme brosme*; and ocean pout, *Macrozoarces americanus*.

Acoustic techniques have become important tools in fishery research in the last 20 years. Of these, sonar has proven useful in a number of related efforts for pelagic fisheries (Forbes and Nakken 1972) including the detection of fishes in the water column (Harden-Jones and McCartney 1962; Anderson and Zahuranec 1977) and estimation of fish numbers and biomass (Smith 1970; Hewitt et al. 1976; Suomala and Lozow 1980; Barans and Holliday 1983; Nakken and Venema 1983). More recent studies have demonstrated how sidescan sonar, in combination with acoustically tagged fish, can be used to evaluate trawling gear (Harden-Jones 1980). Sidescan sonar has been used infrequently to assess critical habitat for demersal fishery resources with the exception of an early attempt to map a herring (*Clupea harengus*) spawning area (Stubbs and Lawrie 1962). Our research has focused on detection of tilefish burrows (Twichell et al. 1985; Grimes et al. 1986; Able et al. 1987), but an outgrowth has been the identification of the habitats of other species. Here we describe the use of sidescan sonar to map the extent and distribution of different habitat types and, in the case of tilefish, derive an estimate of standing stock and potential yield.

TECHNIQUE

Sidescan sonar is similar to low-angle, oblique, aerial photography except that the images (sonographs) are based on differences in the intensity of the reflected acoustic signal rather than the intensity of the reflected light (Belderson et al. 1972). The system consists of a towed vehicle (Fig. 1) in which is housed two sets of transducers that scan to each side, a conducting tow cable, a winch, and a dual-channel recorder for displaying the signals. The transducers are constructed so that their beams form a very narrow arc (1-2°) in the direction perpendicular to the ship's track, but a broad arc in the direction parallel to the ship's track (Fig. 1). As the ship moves, successive bands of seafloor are insonified, and in this way an acoustic areal map is recorded of the scanned area.

We used a 100 kHz Klein[5] sidescan sonar system. This system can resolve features as small as 0.5 m diameter (see Results) at a scanning range of 100 m to each side of the towed vehicle. The

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[5]Use of trade names in this report does not constitute endorsement by the U.S. Geological Survey or the National Marine Fisheries Service.

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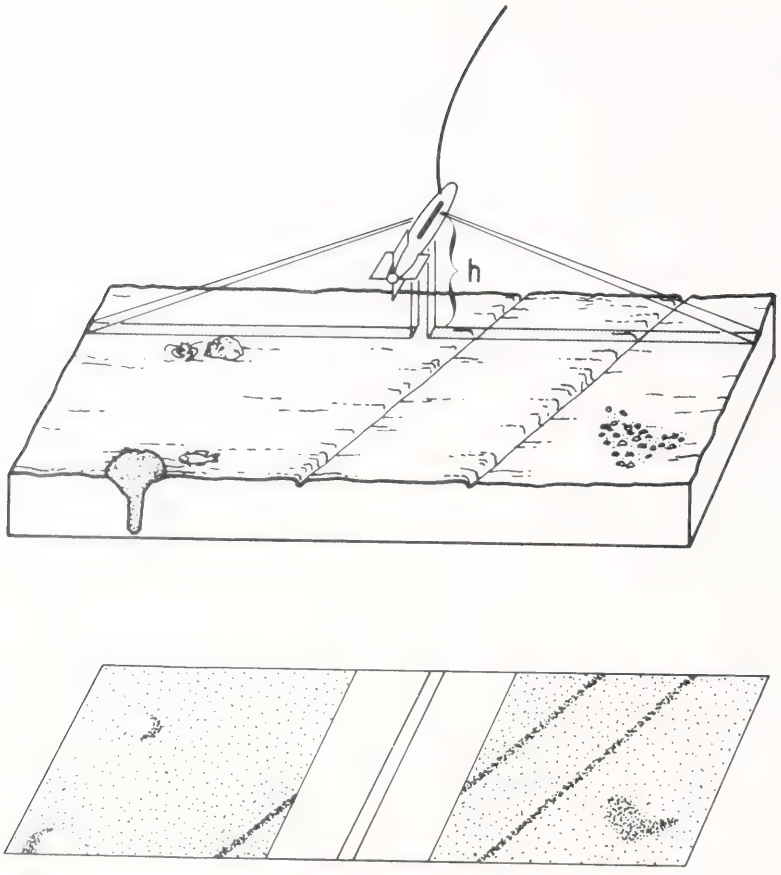

FIGURE 1.—Schematic diagram of a sidescan sonar vehicle being towed over the seafloor (upper) and resulting sonograph (lower) with images of trawl door tracks, tilefish burrow, gravel, and a boulder.

sidescan vehicle was towed 10-15 m above the seafloor at speeds of 3-7 km/hour and was set to scan 100 m or 150 m to each side of the towed vehicle. At these speeds and scanning range, 0.6-1.4 km^2 of seafloor could be mapped per hour.

The sidescan sonograph signatures that characterize different habitat types are largely determined by two conditions, topography and fine-scale roughness (in particular, differences in sediment texture). The signals received from tilefish burrows (Fig. 2) and boulders (Fig. 3) provide good examples of differences in strength of the recorded signal due to topographic effects. A strong signal (dark) is received from the side of the feature facing the transducer while a weak signal or shadow (light) is received from the side sloping away from the transducer. Thus, boulders have the strong return nearest the transducer followed by a shadow (Fig. 3), while burrows appear as a shadow preceding the strong return (Fig. 2). Gravel gives a much stronger signal than silt because of the many small facets facing the transducers. Textural differences usually can be distinguished from topographic differences because there is no shadow associated with them (Fig. 4).

Although the sonograph is a map view of the seafloor, there are two distortions that must be compensated for when interpreting these images. The first is the across-track, slant-range distortion which results from distances being measured from the sidescan vehicle that is positioned above the bottom and not the zero line on the seafloor below the towed vehicle (Fig. 1). For this reason, the point on the seafloor directly below the fish is plotted away from the actual zero line by the distance the fish is off the bottom (distance h on Figure 1). The second geometric distortion is in

FIGURE 2.—Sidescan sonograph of seafloor with vertical burrows of tilefish, *Lopholatilus chamaeleonticeps*, and trawl door tracks in substrate. Heavy arrow denotes direction of incoming sound.

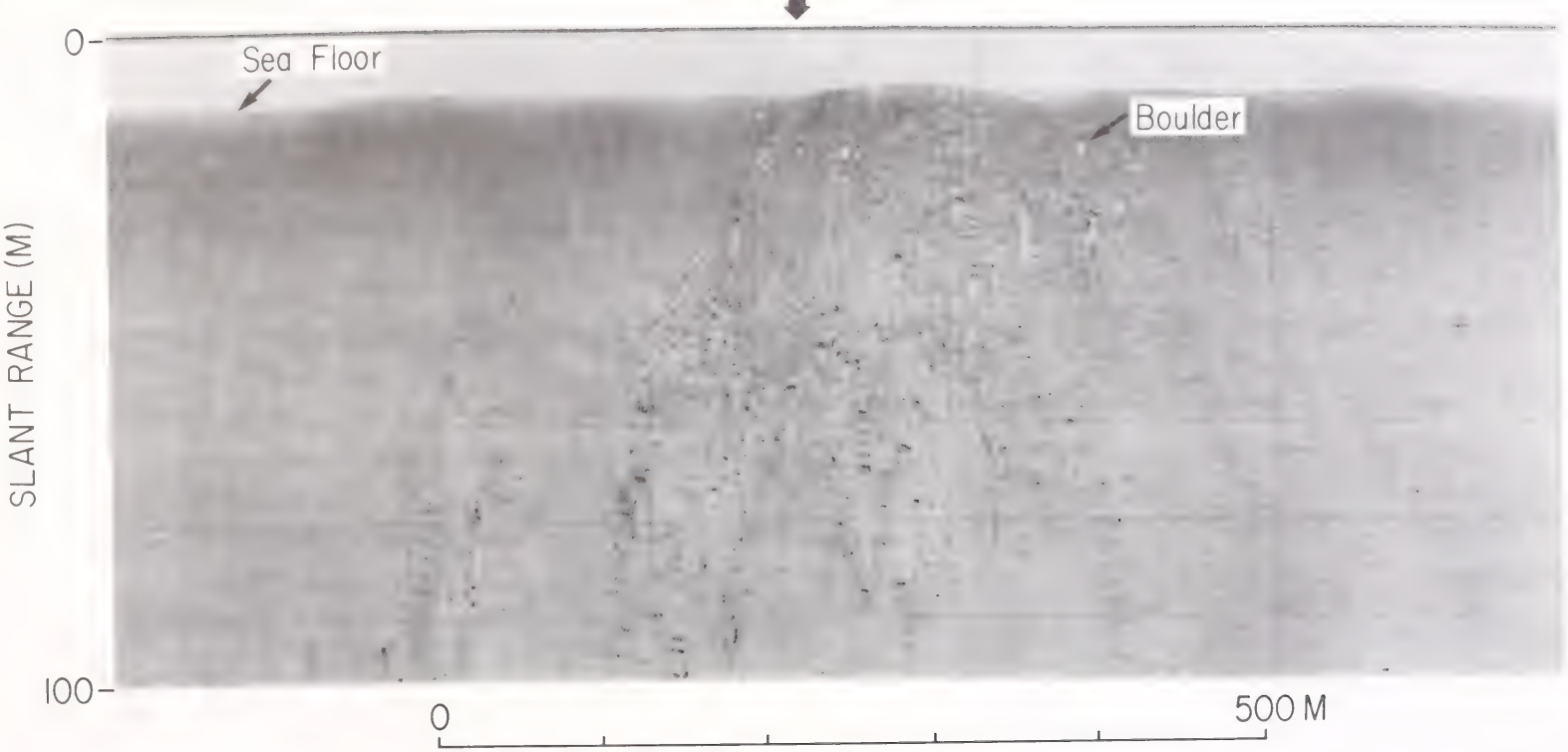

FIGURE 3.—Sidescan sonograph of seafloor in Vineyard Sound with boulders resting on the substrate. Heavy arrow denotes direction of incoming sound.

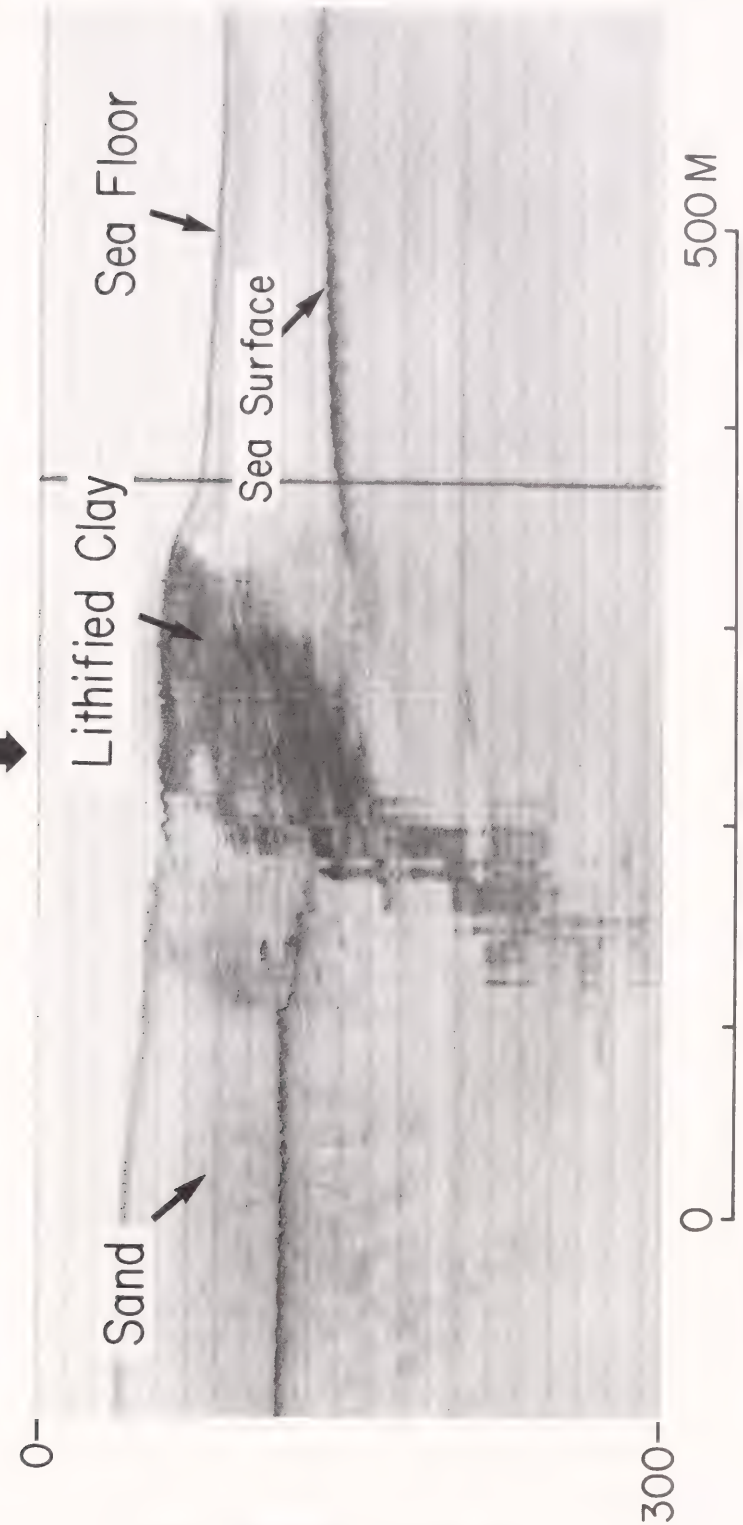

FIGURE 4.—Sidescan sonograph of Lydonia Submarine Canyon wall with outcrop of lithified, burrowed clay likely to be site of pueblo habitat of tilefish and American lobster. Heavy arrow denotes direction of incoming sound.

the along-track direction and is due to the ship's speed. Normally the records are compressed in the direction the ship travelled relative to the true geometry. A circular feature will look elliptical on the sonograph, with the long axis of the ellipse perpendicular to the ship's track, and a linear feature will look more perpendicular to the track than it really is.

RESULTS AND DISCUSSION

The Tilefish Example

Our initial discovery (Able et al. 1982) that tilefish, *Lopholatilus chamaeleonticeps*, construct large (up to 4-5 m diameter and 2-3 m deep), vertical burrows in the substrate (Fig. 5A) suggested that we might be able to detect these burrows with sidescan sonar. Since then we have successfully determined tilefish occurrence, distribution patterns, and relative abundance based on sidescan sonar observations at the edge of the continental shelf in the Mid-Atlantic Bight (Twichell et al. 1985; Grimes et al. 1986) and the upper slope off Florida (Able et al. 1987) (Table 1). Verification of sonograph images as tilefish burrows (Figs. 2, 5A) was accomplished by in situ observations from the *Johnson-Sea-Link* submersibles (Askew 1985) (Table 1).

As a result of these studies, we have demonstrated that sidescan sonar can consistently detect tilefish burrows both where the substrate consists of semilithified clay (Mid-Atlantic Bight: Twichell et al. 1985; Grimes et al. 1986) and softer carbonate muds (off east coast of Florida; Able 1987). During sidescan and submersible operations near Veatch Submarine Canyon, we determined that sidescan sonar could detect tilefish burrows as small as 0.5 m in diameter. Detection of small burrows on sidescan was confirmed when burrows in the area were measured in situ and found to be 35-65 cm in diameter (mean = 48 cm, sample number = 8).

TABLE 1.—Sidescan sonar observations of tilefish, *Lopholatilus* and *Caulolatilus*, burrows on the seafloor off the east coast of the United States.

Location	Date	Sidescan trackline distance (km)	Depth range (m)	No. of verification dives
Vicinity of Hudson Submarine Canyon, Mid-Atlantic Bight	July 1982; August 1983	100	90-200	6
Between Block and Veatch Submarine Canyons, Mid-Atlantic Bight	July-August 1984	129	100-350	2
Off Cape Canaveral, FL	May 1984	36	100-250	2

Under certain situations, tilefish abundance could be estimated directly from sonographs. Usually one tilefish is associated with each burrow (Able et al. 1982), therefore sidescan sonograms providing burrow counts could be used to estimate standing stocks in areas surveyed, with a modification of the area-density method (Everhardt and Youngs 1981). Frequency distributions of burrow density per unit area were log-normal, and there were considerable numbers of zero observations (i.e., about 14-24% zero observations). Therefore we $\log_e$ transformed the burrow density data, and calculated the sample mean and variance of the delta distribution according to Pennington (1983). We present sample estimates from our data for two different locations:

Case 1: Middle Atlantic Bight in the vicinity of Hudson Submarine Canyon (number of observations = 407, number of nonzero observations = 316, data from Twichell et al. 1985) based on the formula

$$N = \frac{B}{a} \cdot A$$

where N = total number of fish (burrows) in surveyed area, $\frac{B}{a}$ = delta-distribution mean number of burrows observed per unit area surveyed, A = total area surveyed, SD = standard deviation, and C.I. (confidence interval) = 95% (1.96 × SD) calculated from the delta-distribution variance, thus

$$N = \frac{2{,}558}{\text{km}^2} \cdot 0.407 \text{ km}^2 \text{ with SD} = 123 \text{ and } 95\%$$

C.I. = 241

$N = 1{,}041 \pm 98$ tilefish [in the surveyed area].

Case 2: South Atlantic Bight off Ft. Pierce, FL (number of observations = 46, number of nonzero observations = 40). The data was obtained with 167 kHz sidescan sonar from the research submersible NR-1 (Able et al. unpubl. data). In this instance

FIGURE 5.—Photographs of A) tilefish, *Lopholatilus chamaeleonticeps*, and American lobster, *Homarus americanus*, in a vertical burrow, and B) tilefish in boulder habitat. These are the same kind of habitats shown as sidescan sonographs in Figures 2 and 3 respectively.

$$N = \frac{369}{\text{km}^2} \cdot 0.42 \text{ km}^2 \text{ with SD} = 64 \text{ and } 95\% \text{ C.I.}$$

$$= 125$$

$N = 154 \pm 53$ tilefish [in the surveyed area].

The estimates of N in cases 1 and 2 could be extrapolated to the entire fishing grounds using an estimate of the area of the entire grounds to provide an estimate of standing stock. However, we believe that extrapolation to areas where no density data is available is imprudent for several reasons. First, the density of burrows in different locations is quite variable as shown in the two above examples, and density on the Middle Atlantic-Southern New England ground (case 1) varies over the grounds at least tenfold (Grimes et al. 1986). Second, some burrows, at least in the Middle Atlantic-Southern New England area, may not be occupied during all seasons of the year (Grimes et al. 1986). Although we do not have as much background knowledge for case 2, we know that burrow density at different sites off the Florida east coast varied at least fivefold (Able et al. unpubl. data).

Another possible source of error in using burrow density to estimate tilefish stock size is that some burrows may be unoccupied. This should be of particular concern in exploited fishing areas. However, Twichell et al. (1985) and Able et al. (unpubl. data) have shown that abandoned burrows are filled by sedimentation relatively rapidly, i.e., less than one year, somewhat ameliorating the problem, at least over longer time periods.

Perhaps the most constructive aspect of cases 1 and 2 is the opportunity to examine the error associated with sidescan sonar estimates of N. These results show that the standard deviation varied from about 5 to 20% of the mean. Hennemuth (1976) found that the standard deviation in the numbers of different demersal species caught per tow within a stratum during stratified bottom trawl surveys approximately equalled the mean. Thus, this comparison suggests that area density estimates of abundance (calculated using the delta distribution) from sidescan sonar surveys will provide abundance estimates of much greater precision than trawl surveys. Reduced manpower needs and rapid application are additional factors that favor the sidescan sonar methodology. However, because the sidescan methodology is only useful for certain three dimensional habitats (e.g., reefs, rocks, and burrows) that would damage or make a trawl useless, application of the two techniques may usually be mutually exclusive.

Tilefish are known to occur in other habitats (Grimes et al. 1986) such as boulder fields, which can be detected on sidescan sonographs (Figs. 2, 5B). Another habitat type (pueblo habitats, Warme et al. 1977; Grimes et al. 1986) occurs in the clay outcrops along the walls of submarine canyons (Figs. 4, 6A). Neither of these habitat types lend themselves to quantification of fish abundance. Recently, we have been able to confirm that the burrows of other tilefish (*Caulolatilus* spp.) are also detectable with sidescan sonar (Able et al. 1987; Figs. 6B, 7). Subsequent observations from a submersible confirmed that these burrows were occupied by *C. microps* and *C. cyanops* with frequent multiple occupancy. Given that it has now been demonstrated that representatives of four of the five genera of tilefishes construct burrows (see Able et al. 1987), it is reasonable to suspect that all tilefish construct burrows. Thus, those larger species of commercial interest, such as red tilefish, *Branchiostegus japonicus japonicus* (Lim and Misu 1974), also may have burrows that are detectable by sidescan sonar.

Other Examples and Possibilities

As an outgrowth of our studies of *Lopholatilus* we have observed other species-specific habitats that can be detected with sidescan sonar. American lobster, *Homarus americanus,* typically occupy scour basins around large boulders (Cooper and Uzmann 1977; Valentine et al. 1980) as do cusk, *Brosme brosme,* and ocean pout, *Macrozoarces americanus* (Valentine et al. 1980; Grimes et al. 1986), and these habitats also are detectable with sidescan sonar. American lobster (Fig. 5) and conger eels, *Conger oceanicus,* (Able et al. 1982; Grimes et al. 1986) have been observed in tilefish vertical burrows as well. Similarly, it would not be surprising if the habitats of other clawed lobsters are detectable with sidescan sonar. For example, *H. gammarus* from the eastern North Atlantic is similar to *H. americanus* in that it is shelter seeking and occurs around boulders (Dybern 1973). In addition, recent in situ observations in the Gulf of Mexico have discovered that yellowedge grouper (*Epinephelus flavolimbatus*) also occupy burrows and elongate trenches (R. S. Jones, E. Gutherz, and W. R. Nelson, pers. obs.) that could easily be detected by sidescan sonar.

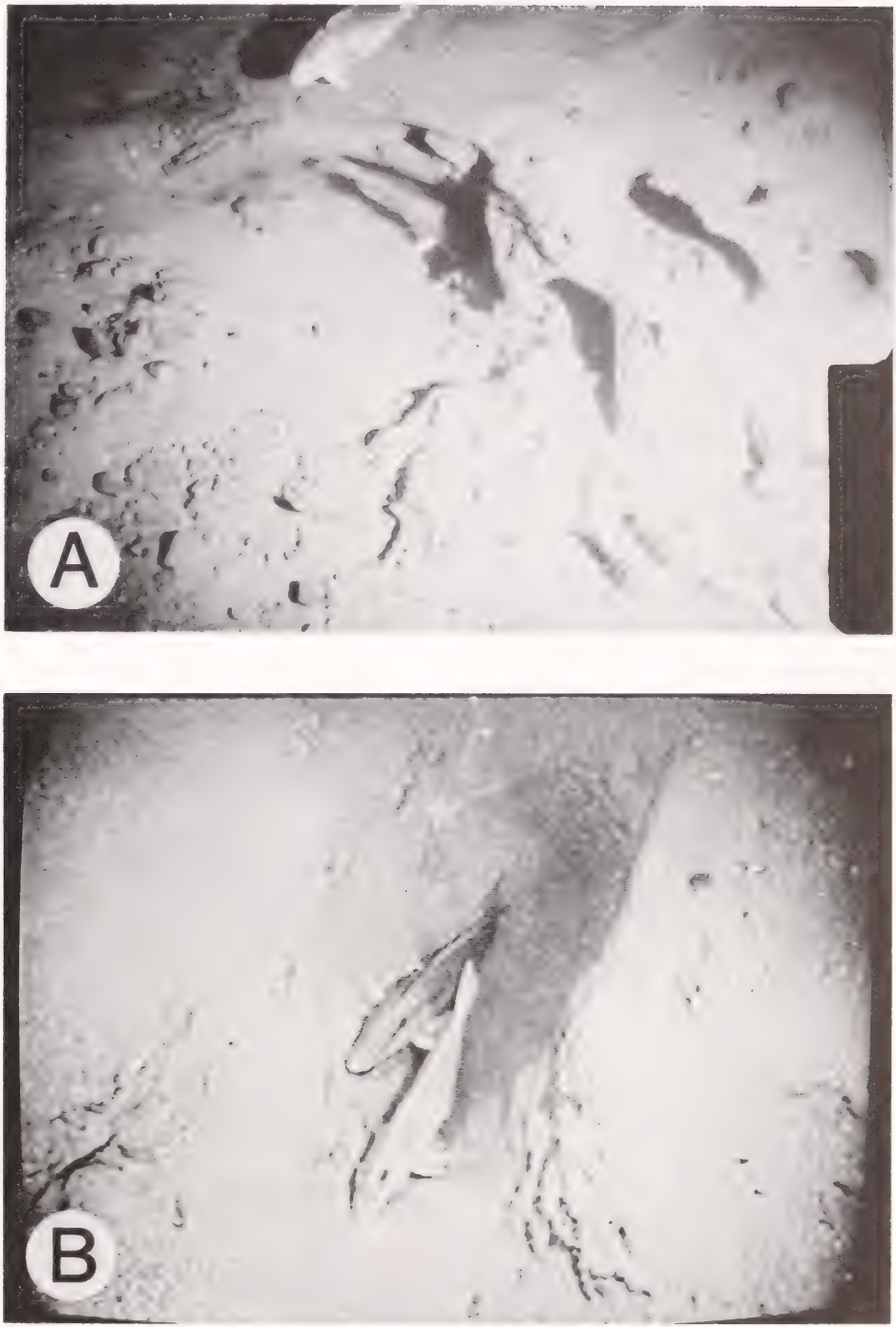

FIGURE 6.—Photograph of tilefish, *Lopholatilus chamaeleonticeps*, in A) pueblo habitat that is part of a clay outcrop and B) *Caulolatilus* tilefish in a burrow. These are the same kind of habitats as shown in Figures 4 and 7 respectively.

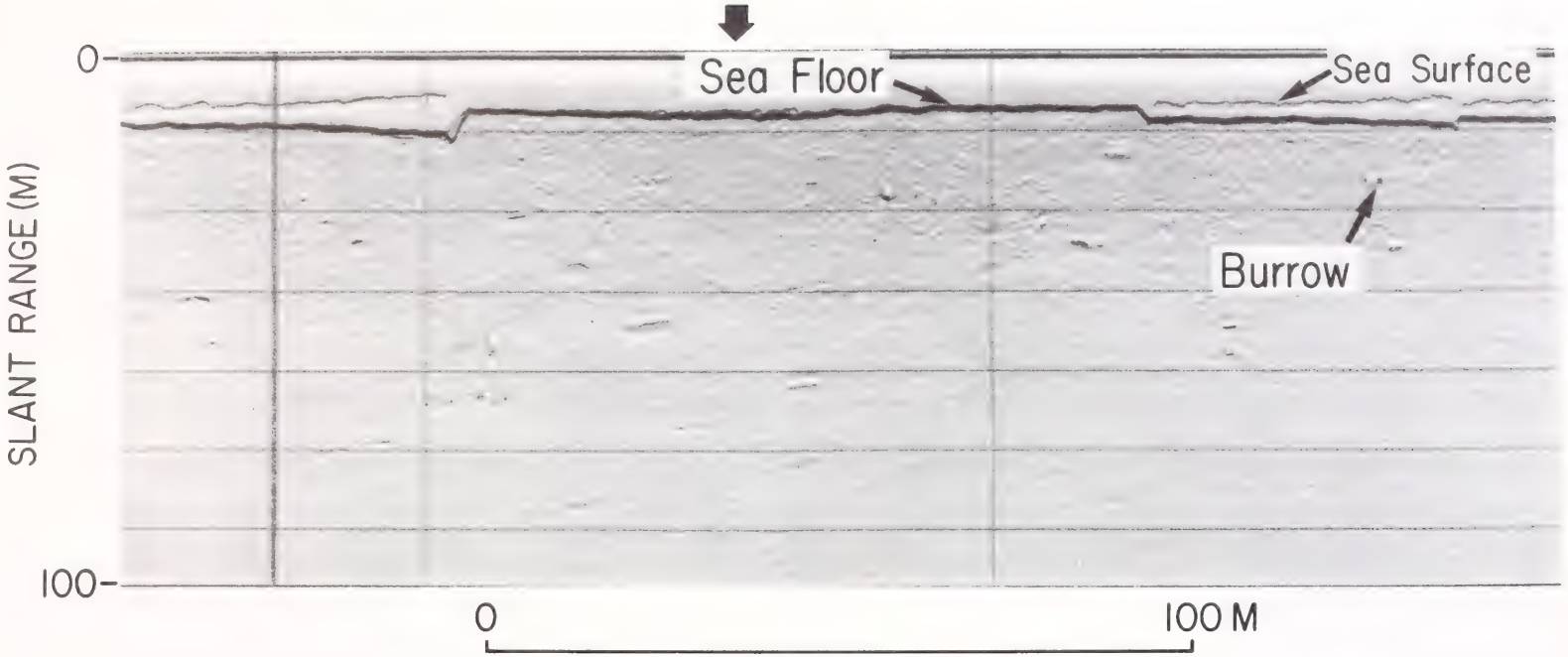

FIGURE 7.—Sidescan sonograph of seafloor with *Caulolatilus* tilefish burrows off Cape Canaveral, FL. The sharp steps in the seafloor trace are where the sidescan was raised or lowered. Heavy arrow denotes direction of incoming sound.

With sidescan sonar, detection and mapping of general habitat types such as rock outcroppings and wrecks, which support populations of commercially important species (e.g., Grimes et al. 1982; Sedberry and Van Dolah 1984), could be done efficiently. Sidescan sonar also could prove very effective (see Wong et al. 1970) in mapping the distribution and relief of a coral reef, and other outcroppings which are often the habitats of groupers, snappers, porgies, and grunts.

In addition to these specific examples, general characteristics of sidescan sonar are advantageous in detecting demersal fish habitats. The system has a wide effective search image (up to 150 m to each side for the 100 kHz Klein sidescan unit) that enables it to map large areas of the bottom during a single transect. With multiple transects a complete picture of the bottom can be obtained. Also, a sonograph could determine potentially appropriate habitats for several species simultaneously. For example, in our studies we have been able to detect boulders (potential lobster, tilefish, and cusk habitat) and vertical burrows (potential tilefish, lobster, and conger eel habitat) in the same transect of the sidescan sonar.

Verification of the various images that appear on the sonograph is critical to successful operation of sidescan sonar for fish habitat detection. We have been able to do this using observations from the *Johnson-Sea-Link* submersibles (Twichell et al. 1985; Grimes et al. 1986; Able et al. 1987). However, this is an expensive option and not generally available. Others have been able to verify sonograph targets from underwater photographs (Bouma and Rappeport 1984) or underwater television (Powles and Barans 1980). The simplest technique, and one that would offer the most information to a fishermen, is directed fishing at the location of sonograph targets of particular interest.

Even with these advantages, sidescan sonar operations are still expensive. However, a considerable body of sonograph data already exists that has not been utilized by fishermen or fishery biologists. A large number of sidescan sonar surveys have been conducted in North American waters in recent years, largely as a result of exploration for oil and related impact studies (Carpenter and Roberts 1979; Neurauter 1979; Carpenter et al. 1982). We have taken advantage of one of these surveys to identify possible tilefish burrows off the west coast of Florida, an area in which we had no prior experience. Individual burrows were clearly visible on sonographs (Neurauter 1979; target type No. 3, fig. 39) originally made to identify geologic bedforms.

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THE EFFECTS OF BOTTOM TRAWLING ON AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, IN LONG ISLAND SOUND

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ABSTRACT

American lobsters taken in the commercial trawl fishery in Long Island Sound, U.S.A., were inspected for incidence of damage and immediate mortality associated with bottom trawling. Similar sampling was conducted in the pot fishery. American lobsters from trawl and pot catches were held in controlled conditions for 14 days to determine the level of delayed mortality associated with the two fisheries. Trawl-caught lobsters were exposed to subfreezing (−9.5°C) temperatures for periods from 30 to 120 minutes and then returned to seawater to determine the rate of freeze-induced mortality. Major damage rates due to trawling ranged from 12.6-14.0% during molting periods to 0-5.6% during intermolt periods. Delayed mortality ranged from 19.2% during the July molt to 1% during August and appeared to be related to the incidence of damage, molt condition, and temperature. Mortality of American lobsters held in subfreezing temperatures occurred after 30-minute exposure and reached 100% at 120-minute exposure.

The American lobster, *Homarus americanus*, supports one of the most valuable commercial fisheries in the northwest Atlantic Ocean with landings of approximately 20,900 t per year valued at $115 million (Anonymous 1985). The fishery is conducted predominantly with traps or pots and, secondarily, with bottom trawl nets.

Long Island Sound is a 2,908 km^2 embayment of the Atlantic Ocean in southern New England, lying between Connecticut and New York at approximately lat. 41°N. The Sound supports a spawning stock of American lobsters and a valuable commercial lobster fishery, which, in 1985, generated landings of 1,134 t valued at $7.0 million for some 900 commercial fishermen. In Connecticut, over 90% of the commercial landings are taken by the pot fishery, and over 90% of Connecticut's commercial fishermen are lobster pot fishermen. Connecticut trawlers, who catch American lobsters in a mixed species bottom fishery, take <10% of Connecticut commercial landings and constitute about 10% of all commercial fishermen taking lobsters. Recreational lobstermen, both potters and scuba divers, totaled 2,440 in 1985 but only accounted for about 5% of total landings (CT DEP[2]).

The resource is heavily exploited with annual exploitation rates ranging from 85 to 95% (Briggs 1985; Blake 1986). Principal management measures include prohibitions on the taking of females bearing external eggs and the retention of any American lobster <81 mm carapace length (CL). These measures are intended to protect American lobsters from exploitation until they have reproduced at least once.

During late 1982, commercial catch per unit effort rates doubled from those of the previous 5 years (CT DEP fn. 2). This increase stimulated a shift in directed fishing by some trawlers from mixed finfish to lobsters. The redirection of effort also generated competition for lobsters and fishing space, and an extremely emotional controversy arose between potters and trawlers. This paper addresses the resource considerations of the controversy, that is, the impacts of mobile trawl gear on lobsters.

This study was designed to measure 1) the physical injury and immediate mortality incurred by American lobsters in the trawl fishery; 2) the potential level of trawl-induced delayed mortality of American lobsters less than the minimum length upon return to the water; and 3) the rate of mortality of American lobsters due to exposure to subfreezing air temperatures during winter fishing.

METHODS

Incidence of Damage

Biologists made 63 trips aboard commercial stern trawlers from 12 to 26 m and 12 trips on pot vessels from 12 to 14 m. Except during January

[1]Bureau of Fisheries, Connecticut Department of Environmental Protection, P.O. Box 248, Waterford, CT 06385.

[2]Connecticut Department of Environmental Protection (CT DEP) unpublished fishery statistics.

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1984, trawl samples were obtained each month from July 1983 through January 1985 during tows of 1-3 h duration. Similar observations of trawl catches were obtained from cruises made by the CT DEP's research vessel (a 13 m stern-rigged trawler) from May through November in 1983 and 1984 during tows of 0.5-2 h duration. Commercial pot fishery sampling was conducted intermittently during summer and fall in both years. All samples were obtained in Long Island Sound west of long. 72°52′W.

American lobsters were examined for evidence of physical damage, denoted as "new" (resulting from the current net tow or pot haul) or "old" (previously sustained). Old damage was inferred by the presence of discolored and healed tissue and by the absence of bleeding. New damage was further categorized as "major" and "minor". Major damage was defined as death, broken or crushed body parts or claw(s), and multiple injuries, even when each individual wound was minor. Minor injury included walking leg loss or damage, antenna damage, minor breakage to a claw or rostrum tip, and recently autotomized claw(s). Recent autotomy (reflex amputation) was defined as a fresh partition without discoloration of the covering membrane at the "breaking plane" (Herrick 1909). Additional data were recorded on length, sex, shell hardness, presence of eggs, and absence of claws. Soft, newshell, and hardshell condition generally followed stages A, B, and C, respectively, as described by Passano (1960). In this paper, the term "newshell" includes both soft and newshell lobsters (stages A and B).

In comparing damage rates between commercial and research vessels, we found that hardshell American lobsters <81 mm CL were damaged more frequently in research than in commercial samples ($\chi^2 = 6.143$). Since the research vessel used a smaller mesh (51 mm cod end) than commercial vessels (75-114 mm cod end), it caught a proportionately greater number of American lobsters <81 mm CL (86% research vs. 72% commercial). Therefore, only lobsters ≥81 mm CL were analyzed because the greater proportion of sublegal American lobsters and other biota in the small mesh sample might have resulted in an overestimate of damage relative to the commercial fishery, due both to intraspecific, agonistic behavior and to compacting of net contents.

The incidence of major damage, compared between pot and trawl gears, large and small trawl vessels, and commercial trawlers and research trawler were analyzed by chi-square goodness of fit (Sokal and Rohlf 1969).

Delayed Mortality

Damaged and undamaged American lobsters less than the minimum length were taken from the same area of Long Island Sound, on the same date, from commercial pot vessels and from either commercial trawl vessels or research vessel. Samples were obtained in November 1983 and May, July, and August 1984. They were transported in tanks with circulating seawater to a laboratory equipped with an open circulating seawater system and were observed twice daily for a period of 14 days. Lobsters were fed daily with assorted fish species. Dead lobsters were removed upon observation. Lobsters were selected nonrandomly from catches to ensure that damaged lobsters were adequately represented in the tests. Since damaged lobsters often made up only a small percentage of the total, our sample consisted of proportionally more damaged lobsters than their actual proportion in the catch.

American lobsters with minor damage were combined with undamaged ones for analysis because undamaged lobsters rarely experienced delayed mortality (2/309) and those with minor damage never did. To estimate total delayed mortality from each gear, the observed delayed mortality rate in each test category (undamaged hardshell, damaged hardshell, and newshell) was extrapolated to the corresponding trawl catches of undamaged, damaged, and newshell lobsters observed during the same months in 1984. The laboratory mortality rate for newshell lobsters was applied to all newshell lobsters in commercial catches rather than only damaged newshell lobsters since internal (unobserved) damage may have occurred. Field data from 1984 commercial catches were used to estimate total trawl-induced mortality because the proportion of newshell lobsters in commercial catches was highest during 1984, and we believe that that year's data most accurately represent the proportion of newshell lobsters taken in the fishery.

The chi-square goodness of fit (Sokal and Rohlf 1969) with Yates' correction for continuity (Zar 1974) was utilized to determine whether lobster mortality rates differed between large and small trawl vessels and between commercial and research trawl vessels. The effect of season and molt condition was examined using a log-likelihood ratio test (G-test; Sokal and Rohlf 1969). Seasonal

changes were defined by water temperature variation whereas molt condition (newshell vs. hardshell) was based on the bimodal distribution of lobster molting (June-July and October-November) observed in Long Island Sound (Lund et al. 1973). The relationship between temperature and shell condition was evaluated by comparing data derived from postmolt periods following the summer (warming seawater temperature) vs. fall (cooling seawater temperature) molts. Postmolt lobsters recovered from the capture process in flowing seawater of 20°C in the July test and 15°-16°C in the November test. Intermolt lobsters in May recovered in 12°C seawater and, in August-September, at 22°C. In all cases, seawater temperatures reported here were elevated approximately 1°-2°C from passage through the circulation system.

The trawl-caught sample included 74 lobsters taken from research vessel catches. Comparison of delayed mortality rates between research and commercial samples revealed no significant difference ($\chi^2 = 0.305$) so the samples were pooled. Delayed mortality rates from samples taken from small (12 m) and large (20 m) trawl vessels in November 1983 and August 1984 were not significantly different ($\chi^2 = 0.05$), therefore, large and small vessel data were also pooled. All damage observations were recorded in the same manner as reported above.

Mortality Due to Freezing

Seventy hardshell, undamaged, trawl-caught American lobsters <81 mm CL were held in an open circulating seawater system at 8°C. On 15 January 1985, three groups of 20 lobsters were exposed in a wooden box (2 m × 1 m × 0.3 m) to ambient air temperature of −9.5°C for periods of 30, 60, and 120 minutes. The remaining 10 lobsters were held without exposure as a control. After the prescribed time had elapsed, the test lobsters were returned to the holding system and observed several times during the following 48-h period for incidence of mortality.

RESULTS

Incidence of Damage Due to Trawling

Damage to American lobsters of all sizes caused by commercial trawling throughout the 19-mo sampling period is summarized in Table 1. The monthly incidence of major damage (including immediate mortality) varied seasonally, from 0 to 14.0% in the trawl fishery and from 0 to 3.5% in the pot fishery. Minor damage ranged from 0.9 to 8.1% in the trawl fishery and from 0 to 10.7% in the pot fishery. Differences between pot and trawl damage rates were compared only for months in which both gears were sampled. The incidence of major damage was significantly greater for trawl samples in July and October-November, but not in August or September (Table 2).

The incidence of damage due to the two gears

TABLE 1.—Incidence of damage to American lobsters taken by commercial otter trawl from July 1983 through January 1985.[1]

Month		Major damage: Broken parts	Major damage: Multiple injuries	Major damage: Dead	No major damage: Minor damage	No major damage: Undamaged	Total (*n*)
Jan.	(*n*)	1	0	2	6	91	100
	(%)	1.0	0	2.0	6.0	91.0	
Feb.	(*n*)	0	0	0	1	14	15
	(%)	0	0	0	6.7	93.3	
Mar.	(*n*)	6	3	0	9	557	575
	(%)	1.0	0.5	0	1.6	96.9	
Apr.	(*n*)	19	8	4	25	1,461	1,517
	(%)	1.3	0.5	0.3	1.6	96.3	
May	(*n*)	22	7	0	21	1,087	1,137
	(%)	1.9	0.6	0	1.9	95.6	
June	(*n*)	1	1	4	2	216	224
	(%)	0.5	0.5	1.8	0.9	96.3	
July	(*n*)	72	44	16	57	854	1,043
	(%)	6.9	4.2	1.5	5.5	81.9	
Aug.	(*n*)	18	4	1	36	1,056	1,115
	(%)	1.6	0.4	0.1	3.2	94.7	
Sept.	(*n*)	49	4	23	36	1,242	1,354
	(%)	3.6	0.3	1.7	2.7	91.7	
Oct.	(*n*)	94	47	25	116	1,426	1,708
	(%)	5.5	2.7	1.5	6.8	83.5	
Nov.	(*n*)	133	128	50	181	1,738	2,230
	(%)	6.0	5.8	2.2	8.1	77.9	
Dec.	(*n*)	77	20	13	68	998	1,176
	(%)	6.5	1.7	1.1	5.8	84.9	

[1]Data from months in successive years are pooled.

TABLE 2.—Incidence of damage to American lobsters taken by commercial pot and otter trawl gears, 1983-84.

Month	Pot fishery: Major damage	Pot fishery: *N*	Trawl fishery: Major damage	Trawl fishery: *N*	χ^2
July	0.9%	2,165	12.7%	1,043	212.2**
August	1.3%	1,512	2.1%	1,115	1.8
September[1]	3.5%	424	5.9%	1,344	2.4
Oct.-Nov.[1]	0.6%	661	14.4%	2,672	96.8**

**significantly different ($P < 0.001$).
[1]1983 data only (no pot fishery samples taken in 1984).

was analyzed with respect to shell hardness and carapace length (<81 mm vs. ≥81 mm). Size-specific damage to newshell American lobsters taken in the trawl fishery was significant with smaller lobsters incurring more damage (43% vs. 30%, $\chi^2 = 6.64$, $P = 0.01$). There were no size-specific differences in damage to newshell lobsters taken in the pot fishery or to hard-shelled ones in either fishery.

Trawled egg-bearing female American lobsters (always hard shelled) incurred 1.9% major damage, no immediate mortality, and 2.1% minor damage throughout the sampling period ($n = 909$). Eggbearers ≥81 mm CL ($n = 585$) exhibited 2.2% major damage and 2.4% minor damage while those <81 mm CL ($n = 306$, 18 size unspecified) incurred 1.3% major damage and 1.6% minor damage. Pot-caught eggbearers sustained 0.9% major, and 0.8% minor damage throughout the sampling period ($n = 1,926$). One of 1,926 pot-caught egg-bearers (0.05%) died on deck. These data suggest that the damage and immediate mortality to gravid American lobsters associated with both fisheries is minimal.

From September 1983 through December 1984, trips were made with both large (15-26 m) and small (12-14 m) trawl vessels during eight different months. In two of those months, damage rates were equal, in two they differed by <1%, and in four they ranged from 7.3% higher for small vessels to 13.7% higher for large vessels. The difference exhibited in the four months for which deviations of more than 1% were observed was not significant ($\chi^2 = 0.019$, $P < 0.5$) indicating that damage to trawled American lobsters is independent of vessel size.

Trawl-induced damage occurred at similar rates in cold-water vs. warm-water intermolt periods (2.2% January-June vs. 3.1% August-September) and between cooling and warming postmolt periods (11.5% October-December vs. 12.6% July; Table 1). This suggests that damage due to trawling is more a function of shell condition than water temperature.

Delayed Mortality

From November 1983 to August 1984, 526

TABLE 3.—Estimated mortality to American lobsters <81 mm CL (delayed and immediate) due to otter trawling in 1984. Actual delayed mortality is computed by multiplying the percent occurrence of each damage category in trawl catches by the laboratory delayed mortality rate for that category. Total mortality rate is the sum of the actual delayed mortality plus immediate mortality observed on deck.

Month	Trawl catches %	Laboratory delayed mortality rate %	Actual delayed mortality %	Observed immediate mortality %	Total mortality rate %
May ($N = 608$, trawler catches; $N = 41$, laboratory samples)					
Hardshell					
undamaged	96.5	0	0	0	0
damaged	2.0	85.7	1.7	0	1.7
Newshell	1.5	33.3	0.5	0	0.5
			2.2	0	2.2
July ($N = 533$, trawler catches; $N = 40$, laboratory samples)					
Hardshell					
undamaged	81.8	10.5	8.6	0	8.6
damaged	9.9	85.7	8.5	2.1	10.6
Newshell	6.2	33.3	2.1	0	2.1
			19.2	2.1	21.3
August ($N = 456$, trawler catches; $N = 146$, laboratory samples)					
Hardshell					
undamaged	98.2	0	0	0	0
damaged	0.7	85.7	0.6	0	0.6
Newshell	1.1	33.3	0.4	0	0.4
			1.0	0	1.0
November ($N = 408$, trawler catches; $N = 147$, laboratory samples)					
Hardshell					
undamaged	86.3	0	0	0	0
damaged	3.9	42.4	1.7	1.2	2.9
Newshell	7.8	33.3	2.6	0.8	3.4
			4.3	2.0	6.3

American lobsters <81 mm CL, taken from pot and trawl vessels, were held to estimate trawl-induced delayed mortality (Table 3). Of 374 trawl-caught lobsters held in the laboratory, 47 (12.6%) had sustained major damage. Eighteen were newshell and were treated as one category regardless of damage sustained. Two of 309 (0.6%) undamaged, hardshell trawl-caught lobsters died whereas 55.3% of damaged ones died within the 14-d period, most within the first 7 days. Six of 18 newshell lobsters died (33.3%). Of 153 pot-caught lobsters, 8 (5.2%) had major damage; none were newshell. No pot-caught lobsters experienced delayed mortality.

Laboratory delayed mortality rates for damaged hardshell American lobsters were pooled in May, July, and August because of the small sample sizes ($n = 14$). Delayed mortality rates ranged from 50 to 100% in the three months. The mean (85.7%) was applied to the proportion of damaged hardshell lobsters in the commercial trawl fishery in each of those months. In November, a 42.4% delayed mortality rate ($n = 33$) was applied to the damaged lobster category in November commercial samples. Although only two undamaged hardshell lobsters died, both occurred in July (2 of 19). This proportion (10.5%) was applied to the proportion of undamaged hardshell lobsters in the July commercial catches. Since no delayed mortality occurred to undamaged hardshell lobsters in May, August, or November, no delayed mortality rate was applied to that category for those months. The delayed mortality rate for newshell lobsters (33.3%, $n = 18$) was applied to the proportion of newshell lobsters in commercial catches (1-8%). Immediate (on-deck) and delayed mortality rates for lobsters <81 mm CL and for each shell condition (undamaged hard, damaged hard, and newshell) were summed, resulting in an estimate of total mortality for each season (Table 3).

Estimated trawl-induced mortality rates for the four sample periods were tested to determine the relative importance of high seasonal water temperatures (July and August) and molting (November and July). November and July had significantly higher rates of mortality than May and August (Tables 3, 4), indicating that molt condition (July and November) is more important in determining the extent of mortality than water temperature. There was no significant difference between May and August delayed and immediate mortality estimates (Table 4) despite a 10°C difference in water temperature. However, warm temperatures appeared to increase the incidence of mortality after molting since the July rate was significantly higher than the November rate (21.3% vs. 6.3%, Table 4).

TABLE 4.—Log-likelihood ratio test of expected trawl-induced mortality to American lobsters <81 mm CL, by season. Underlining denotes no significant difference at $P = 0.05$. $\chi^2 = 178.4^*$ overall, 44.8^* (July-November), 11.8^* (November-May), and 1.8 (May-August).

	May	August	November	July
Water temperature	cold	warm	cold	warm
Molt condition	nonmolting		molting	
Estimated mortality	2.2%	1.0%	6.3%	21.3%

$^*= P < 0.005$.

Mortality Due to Freezing

Exposing undamaged American lobsters to ambient air temperatures of −9.5°C produced no mortality at 30-min exposure, and 70% and 100% mortality at 60 minutes and 120 minutes, respectively. Damaged lobsters were not tested since they occur so infrequently during cold-water periods of the year (Table 1). Freezing temperatures may also induce reflex amputation (autotomy) of claws. One lobster of 20 in the 30-min sample and four American lobsters of 20 in the 60-min sample autotomized one claw.

DISCUSSION

Jamieson and Campbell (1985) found that sea scallop dragging in eastern Canada could damage American lobsters, but since the sea scallop and lobster fisheries generally were not simultaneous (lobsters tended to emigrate from the scalloping areas each season prior to the advent of the drag fishery), the use of scallop gear over beds that hold lobsters at other times posed no significant impact to the resource. Scarratt (1972) observed a similar situation in the eastern Canadian Irish moss rake fishery. Although American lobsters did suffer damage from the gear, most lobsters emigrated before the moss harvest season, so the damage associated with the gear was minimal. In western Long Island Sound, the lobster pot and mixed species trawl fisheries both operate throughout the year. Since the seabed in this area is relatively uniform and generally free of

obstructions to trawling, lobsters can be taken simultaneously with both gears, raising concerns that trawl gear is detrimental to the resource.

In Narragansett Bay, RI, using a 13 m stern trawl-rigged research vessel, Ganz (1980) found low immediate mortality to trawl-caught American lobsters and low damage rates during intermolt periods, and higher damage rates immediately following molting. He observed that hardshell lobsters were not likely to sustain critical injuries but postulated that commercial-scale operations might produce higher damage rates than the research vessel because of net compaction. We found that major damage (including immediate mortality) was greatest during molting periods, ranging from 12.6% in July to 14.0% in November. Hardshell (intermolt) lobsters suffered little damage by commercial trawling, with the monthly incidence of major damage and immediate mortality <3% from January through June and in August. Minor damage, including autotomy of claws, ranged from 0.9 to 8.1% and was greatest in October-November. Minor damage was <2% from March through June.

The incidence of immediate mortality by month never exceeded 0.5% in the pot fishery or 2.2% in the trawl fishery. Moreover, we found that damage rates were independent of vessel size, whether in the commercial fishery or between 12 m commercial and 13 m research vessels (see below). Newly molted American lobsters were damaged by both trawl and pot gears but trawling caused greater damage.

Spurr (1978) found experimental otter trawl-induced injury in summer to be greater in July than in September; however, since he aggregated minor damage with major damage and did not provide sample sizes, quantitative comparison of major damage between the two studies is not possible. Spurr concluded that lobster damage due to trawling in winter would be minor, a conclusion supported by our data.

Ganz (1980) suggested that damaged, sublegal American lobsters might suffer mortality upon release, although he did not investigate this possibility. We found that delayed mortality appeared to be influenced by the condition (incidence of damage) of American lobsters. Only 2 of 309 undamaged, hardshell lobsters experienced delayed mortality after trawling, compared to 26 of 47 (55.3%) damaged, hardshell, trawl-caught lobsters. Delayed mortality never occurred to lobsters with minor damage or autotomized claws. Although the sample size was small ($n = 18$), only one-third of all trawled newshell American lobsters experienced delayed mortality.

While both trawl and pot gear damage lobsters, trawl-caught lobsters alone sustained delayed mortality. One of the initial concerns about trawling was that visibly undamaged American lobsters less than the minimum length, returned to the water after trawling, would suffer a high level of unobserved mortality. Our results indicate that such mortality rarely occurs to undamaged American lobsters; consequently, potential delayed mortality may be ascertained simply by inspection of the incidence of major damage in the catch.

Of the two molting periods in Long Island Sound, a higher rate of mortality was observed in July than in November, possibly related to the warmer postmolt water temperatures which occur in summer compared with late fall. Damage rates during postmolt periods were similar (12.6% July vs. 14.0% November) notwithstanding the difference in water temperature. These results suggest that the resistance of trawled postmolt American lobsters may be lowered by warm seawater temperatures and that such temperatures may increase the occurrence of delayed mortality independent of the incidence of damage. Mean values of immediate and delayed mortality for all samples taken during intermolt periods were negligible (<1.0% and <2.0%, respectively).

There appeared to be some variability in mortality depending on the type of damage sustained. Damage to the abdomen and carapace was almost always lethal (100% and 92%, respectively), while broken parts such as claws or rostrum resulted in 25% and 50% mortality, respectively. However, small sample sizes precluded definitive analysis.

Ganz (1980) speculated that the most significant impact of trawling might be related to the cumulative effect of trawling and damaging sublegal American lobsters, and subsequently releasing them to be taken again. In discussing this possibility, he reported an immediate claw loss (cull) rate of 3.5% and a prior cull rate of 8.8%. This is a valid concern, and one which should be considered in both trawl and pot fisheries. For example, Smith (1977) reported a cull rate of 26% in an area of Long Island Sound which had not been trawled during recent years and a rate of 23% in an area lightly fished with trawls, suggesting that a high cull rate can occur in the absence of trawling (both areas were heavily fished with pots). These observations, while higher than Ganz's, included both new and old claw loss as well as lobsters with regenerated claws. In the

present study, minor damage (which included immediate claw loss) ranged from 0.9 to 8.1% per month in the trawl fishery and from 0 to 10.7% in the pot fishery.

While the mortality of trawled newshell American lobsters was high during the two molting periods, they represented such a small percentage of the total trawl catch (1-8%) that the estimated total mortality to the entire catch was little changed by their presence. Similarly, while damaged lobsters sustain a high rate of mortality, it is their proportion in the catch which determines the rate of additional mortality experienced by the population.

No truly soft American lobsters (stage A, after Passano 1960) were observed in the pot catches sampled for delayed mortality estimates, and they occurred rarely in other commercial pot samples (up to 3% in July 1984). They were observed infrequently in trawl catches as well (up to 7.8% in November 1984). The low incidence of soft lobsters in commercial catches is probably due to reduced mobility during the shell hardening process (Herrick 1909) when American lobsters are most vulnerable to damage and predation.

No significant difference was observed in damage rates or delayed mortality based on sampling of vessels <15 m or >15 m. There was no difference in delayed mortality rate between 13 m research vessel samples and either 12 m commercial or 15-26 m commercial trawlers. Finally, there was no difference between damage rates to American lobsters ≥81 mm CL taken by research and commercial vessels in October-November 1984, the only period for which comparable data (tows of 2-h duration) were available for both vessel categories. The former results suggest that trawl-induced damage and mortality is independent of vessel size; the latter suggests that observations of fishery-induced damage made by biologists were representative of actual fishing conditions.

While American lobsters may succumb to subfreezing air temperatures, consideration of this source of mortality is a function of both temperature and exposure time and must be judged on the behavior of the fishery in question. Edwards and Bennett (1980) reported a survival rate of 42-85% for *Nephrops norvegicus* after 1-h exposure to air, noting that favorable weather conditions and the type of vessel used were factors contributing to higher survival. In the present study, American lobsters exposed to −9.5°C air temperatures for 30 minutes all survived. Those exposed for 120 minutes all succumbed. Intermediate exposure (60 minutes) produced intermediate results (30% survival). In Long Island Sound, field observations during a 19-mo period suggested that operators in the trawl fishery commonly sorted the catch within 15-45 minutes.

Our design tended to maximize the debilitating effect of freezing temperatures. Trawl net contents are commonly released onto the vessel deck in a pile. Consequently, organisms on the inside of the pile are protected from cold air temperatures. In our test, all American lobsters were placed on a flat table with 0.3 m high sides; thus, all lobsters were equally exposed to freezing temperatures and none were able to benefit from the "piling" of a normal catch. As a consequence, this experiment very likely overstated the impact of subfreezing air temperatures on commercially taken American lobsters.

An additional consideration beyond the directed fishery is the mortality to "sublegal" American lobsters (those <81 mm CL) and the damage to lobsters during molting periods which may result from a mixed species trawl fishery which includes a so-called incidental catch or "bycatch" of lobsters. As with freeze-induced mortality, this factor must be judged based on the performance of the fishery in question.

In Connecticut, trawlers reported <10% of the commercial American lobster landings reported by all fishermen during the period 1982-86 (CT DEP fn. 2). However, given the controversy surrounding trawling during this investigation and the weaknesses inherent in catch reporting systems during periods of controversy (Matlock 1986; Ferguson 1986), a number of independent methods of observation were used to determine the actual impact to the resource associated with trawling. Unannounced boardings by Connecticut Conservation Officers were utilized to estimate the true magnitude of lobster catches. Biologists made sampling trips on the vessels of commercial trawl fishermen fishing in Long Island Sound to document the fishery-induced incidence of damage. Research vessel sampling was used to estimate a fishery-independent rate of trawl-induced damage. The results of these observations suggested that the magnitude of American lobster catches per trip was about the same as those reported in mandatory logbooks and, except during molting periods, trawl-induced damage was minimal.

Observations in controlled laboratory conditions were utilized to estimate the delayed

mortality which might be expected to occur to sublegal American lobsters returned to the water after trawling. These observations indicated that this source of mortality should only be a concern during molting periods. Since delayed mortality to sublegal American lobsters occurs to a significant degree only during molting periods, an incidental limit of some number of lobsters per day for trawlers during those periods represents an effective means to deter the directed fishery and protect sublegal American lobsters while allowing the finfish fishery to continue.

There has been considerable controversy in New England regarding the effects of trawling on the American lobster resource. This study provides three results of assistance to fishery managers dealing with this question. First, both pot and trawl gear damaged American lobsters, but trawl-induced damage occurred more frequently, and particularly during molting periods. However, damage was not always lethal and visibly undamaged lobsters virtually never sustained delayed mortality. Second, during molting periods, mortality caused by trawling reached 6-21%, depending on season. Delayed mortality was influenced most by the degree of damage sustained by the lobster. Therefore, while delayed mortality may be of considerable consequence to the resource during molting periods, it can be estimated by inspection of the condition of lobsters in the catch. Third, during intermolt periods, both immediate and delayed mortality due to trawling occurred infrequently ($<1\%$ and $<2\%$, respectively). All these factors should be evaluated within the context of the biological and socioeconomic considerations inherent in the fishery management process.

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FACTORS AFFECTING COOKED TEXTURE QUALITY OF PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, FILLETS WITH PARTICULAR EMPHASIS ON THE EFFECTS OF INFECTION BY THE MYXOSPOREANS *KUDOA PANIFORMIS* AND *K. THYRSITIS*

GEORGE KUDO, HAROLD J. BARNETT, AND RICHARD W. NELSON[1]

ABSTRACT

Pacific whiting is known to have abnormal cooked texture induced by enzymes of the Myxosporean parasites *Kudoa*. An extensive United States-Canadian joint research project was initiated to explore the correlation between texture quality and intensity of *Kudoa* infection. Enumeration of white and black pseudocysts and identification of the *Kudoa* species present was done by the Canadian team while texture quality was determined by the U.S. team. Data analysis showed that 1) white pseudocysts were more closely correlated with cooked texture quality than were black pseudocysts; 2) *K. paniformis* and mixed infections correlated well with sensory texture while *K. thyrsitis* infections correlated poorly; 3) Pacific whiting from southern fishing areas had higher white pseudocyst counts of *K. paniformis* and more soft abnormal texture than Pacific whiting from northern fishing areas; 4) nape and dorsal areas of fish had higher intensities of *Kudoa* infections and greater incidences of abnormal texture; 5) body length correlated weakly with texture quality, but there was no relationship between sex and sensory texture. Results of experimental evaluations indicate that the visual culling method may have some potential for use in sorting Pacific whiting with white and/or black pseudocysts. However, the white pseudocysts require careful examination to be detected. Therefore, a visual culling method may be too time consuming to be practical for use on a production line.

Between 1982 and 1984, the annual catch of Pacific whiting[2], also known as Pacific hake, *Merluccius productus*, harvested by American and foreign fishing fleets in the territorial waters off the Pacific coast of the United States, ranged between 80,000 and 100,000 t. Of this amount, between 67,000 and 79,000 t were annually harvested by a joint venture fishery with the Soviet Union. The catch by other foreign countries, mainly Poland and Bulgaria, operating in the directed fisheries, ranged from 7,000 to 14,000 t[3]. Although the Pacific whiting resource has been estimated to vary between 445,000 and 3,440,000 t (Dark 1985), its domestic use has been limited because of soft texture associated with the presence of a parasitic Myxosporea of the genus *Kudoa*. Patashnik et al. (1982) and Tsuyuki et al. (1982) established that the flesh deterioration of infected Pacific whiting was due to an enzyme-induced proteolysis. However, the correlation between the degree of infection and the condition of the flesh was not entirely clear. Sometimes Pacific whiting heavily infected with the protozoan parasite appeared, when cooked, not to be affected, i.e., soft-textured, while lightly infected fish had very poor textures. The discovery by Kabata and Whitaker (1981) that Pacific whiting is infected by two different species of *Kudoa* (Fig. 1) explained some of these discrepancies. Tsuyuki et al. (1982) found that these species, *Kudoa paniformis* (Kabata and Whitaker 1981) and *Kudoa thyrsitis* (Gilchrist 1924), differ from each other in their enzyme activity, i.e., enzyme-induced proteolysis. Because Pacific whiting can be infected with one or both species of *Kudoa*, the final condition of the flesh might be determined by the type of *Kudoa* since *K. paniformis* is capable of producing much heavier infections than *K. thyrsitis* (Kabata and Whitaker 1981).

From a public health standpoint, no protozoan diseases of fish have been known to have man as host (Oppenheimer 1962) and myxosporea per se have never been reported to cause illness in humans (Konagaya 1982; Nagahisa et al. 1983). Nonetheless, infection with *Kudoa* continues to

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[2]The U.S. Food and Drug Administration has ruled that this species can be marketed as Pacific whiting (Robins et al. 1980).

[3]W. Daspit, OFIS, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115, pers. commun. March 1985.

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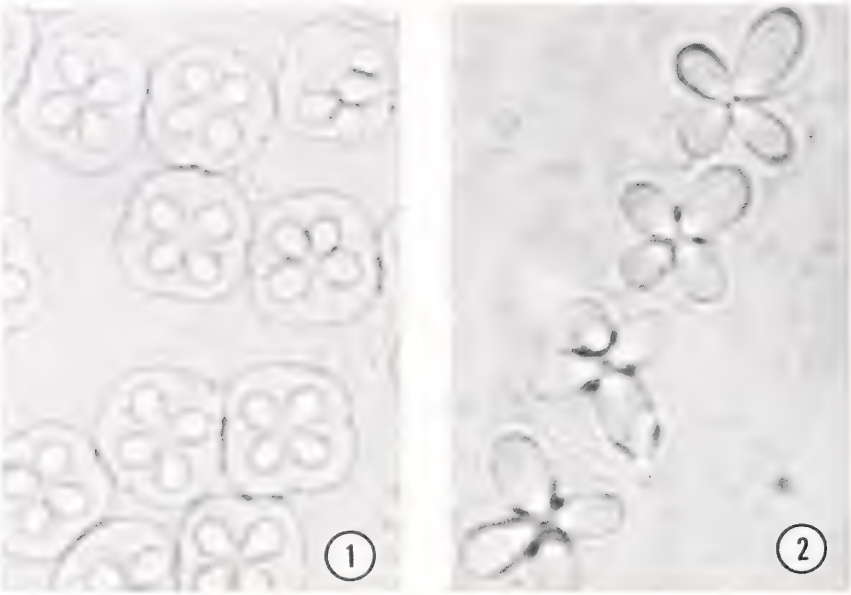

FIGURE 1.—Unstained spores at ×2400, (1) *Kudoa paniformis* (approximately 8 μm in size) and (2) *Kudoa thyrsitis* (about 15 μm in size), found in the muscle of Pacific whiting. *Photo by Carla Stehr.*

be a serious limiting factor in the Pacific whiting fishery.

A joint U.S.-Canadian project aimed at taking the full measure of these problems was initiated in 1983. The purpose of this paper is to report on the results of investigations into cooked flesh texture and its relationship to the intensity and type of *Kudoa* infection. The paper also correlates subjective sensory texture values with objective instrumental readings and establishes texture quality profiles of fish taken in different geographic areas along the distribution range of the Pacific whiting. Other factors, such as sex, body size, and location of infection within the various parts of the fish (i.e., anterior, posterior, dorsal, ventral) which might influence texture quality, were also examined. Finally, visual culling was evaluated to determine if sorting Pacific whiting infected with pseudocysts from the pack was practical.

MATERIALS AND METHODS

The sample used in this investigation consisted of 579 Pacific whiting collected by National Marine Fisheries Service personnel aboard the chartered MV *Nordfjord* in 37 hauls off the Pacific coast of North America, between lat. 37°18′N (near San Francisco) and 48°54′N (west coast of Vancouver Island) in the four International North Pacific Fisheries Commission (INPFC) areas (Fig. 2). The fish were caught between 16 July and 28 September 1983, in 30-min tows at depths ranging from 34 to 164 fathoms. Water temperatures at the cod end ranged between 7.5° and 10.5°C, while surface temperature ranged between 12.1° and 18.8°C. These temperatures were somewhat warmer than those in previous years, due to the 1982-83 El Niño effect (Weinberg et al. 1984). The Pacific whiting catch varied from 7 to 2,053 kg in the total catch of 20 to 2,488 kg per haul (Weinberg et al. 1984). A 32 mm (1 1/4″) stretched mesh size cod end liner was used to retain small fish. Each fish was measured and sexed, individually numbered, and frozen aboard the vessel. The fish samples were taken to the Utilization Research Division (URD) laboratory of the Northwest and Alaska Fisheries Center (NWAFC) in Seattle where they were sectioned longitudinally and each half labeled accordingly. One half of each fish was shipped to the Pacific Biological Station in Nanaimo, B.C., Canada, for parasitological examination, and the other retained by the URD laboratory for determination of flesh quality.

The parasitological methods used by the Pacific Biological Station are described elsewhere (Kabata and Whitaker 1986). Intensity of infec-

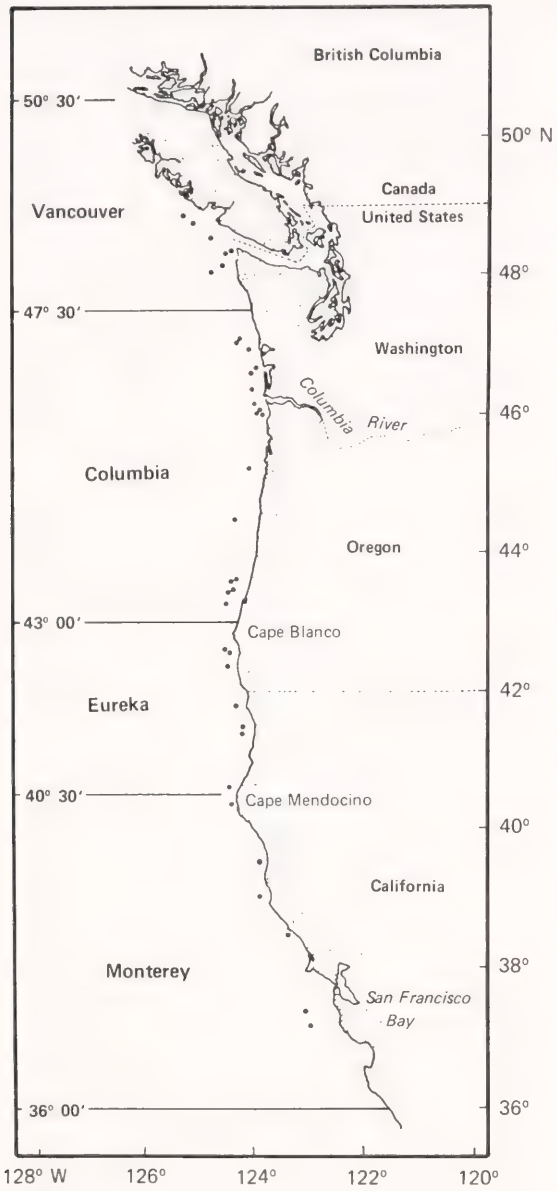

FIGURE 2.—Locations of the 37 hauls (black dots) of Pacific whiting made by MV *Nordfjord* and the International North Pacific Fisheries Commission (INPFC) areas surveyed in the summer of 1983.

tion with *Kudoa* was measured in each fillet, which were divided into six inspection areas (Fig. 3) as numbers of pseudocysts (i.e., infected muscle fibers) per gram of tissue. Separate counts were taken for each species of *Kudoa* and for white (young) and black (old) pseudocysts.

The flesh texture was determined in two ways: 1) by a sensory technique developed especially for Pacific whiting and 2) by mechanical shear press. The sensory texture evaluations were made by two project personnel experienced with Pacific whiting texture. Normal taste panel methods could not be used in this study because each sample fillet was divided into six areas for sequential evaluation, similar to the method described by Patashnik et al. (1982). The project personnel used a combination of taste and touch techniques to determine hardness sensation. The touch technique consisted of estimating hardness or resistance by pressing on the sample with the tip of the index finger. Taste texture was determined by the subjective force required to bite through the sample with the molar teeth.

Texture ratings were based on a 9-point hedonic scale (Table 1) where scores of 9 to 5 described normal textures ranging from the firmness of rockfish to the tenderness of typical Pacific whiting, 4 to 3 as the softness of sole, and 2 to 1 as an abnormal or mushy to liquefied texture.

Prior to measuring sensory textures, the frozen Pacific whiting halves were placed on racks in trays, tempered at ambient temperature for approximately 2 hours or until semifrozen, covered with aluminum foil, and then, depending on the

TABLE 1.—Sensory texture category based on a 9-point hedonic scale.

Category	Scale	Description
Normal	9	Very firm and flaky as in rockfish
	8	Very firm and flaky as in rockfish
	7	Firm and flaky as in true cod
	6	Tender and slightly flaky as in typical Pacific whiting
	5	Tender and slightly flaky as in typical Pacific whiting
Soft	4	Soft as in sole and flounder
	3	Soft as in sole and flounder
Abnormally soft[1]	2	Mushy
	1	Liquefied

[1]Considered organoleptically unacceptable as previously described by Patashnik et al. (1982) and Nelson et al. (1985).

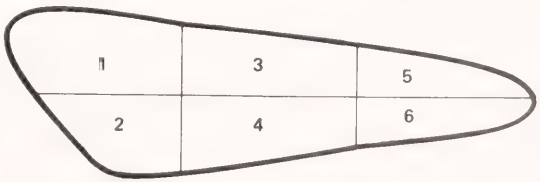

FIGURE 3.—Selected Pacific whiting fillet areas examined for cooked texture and pseudocyst intensity.

thickness, cooked in an oven at 375°F for 20 to 50 minutes. The texture of the fish was then determined organoleptically.

Mechanical texture was determined on 180 randomly selected fish, in which duplicate shear press readings were taken on 15 g of muscle tissue removed from the dorsal portions of the fish samples to correlate with the portions taken for sensory evaluations. The successful use of mechanical texture analysis to correlate with the sensory texture of Pacific whiting was previously reported by Nelson et al. (1985). The tissues were teased into flakes which were leveled to a height of 8 mm in a Kramer shear-compression cell which was reduced in size to 29 mm wide, 71 mm long, and 64 mm deep to accommodate the sample. The assembly, consisting of four blades, was similar to the one described by Bilinski et al. (1977) and used by Tsuyuki et al. (1982) to evaluate objectively the texture of Pacific whiting. The cell operated in conjunction with the Food Technology Corporation FTA 3000 transducer[4], TP-4 Texturepress, and the TR-5 Texturecorder. A plot was made of the force required to drive the blades through the sample at a ram speed of 1 cm per minute and at a set recorder range. The peak force in pounds per 15 g tissue was calculated from the plot (Bourne 1982).

Culling was performed on partially thawed halves of fish. Pseudocysts are visible as white or black threads of varying intensities imbedded longitudinally along the muscle fibers. The culling categories were modeled after the scheme of Patashnik et al. (1982) for both white and black pseudocysts as none, light (<20%), moderate (20 to 30%), and heavy (>30%) as determined visually, based on the percent area of fillet affected.

Only fish over 27 cm were used for all analyses, since in commercial operations fish smaller than 27 cm would not likely be taken because domestic and foreign fishermen use 50 mm (2 in) to 100 mm (4 in) cod end mesh size as regulated by the Pacific Coast Groundfish Fishery Management Plan.[5]

Data representing sensory textures and *Kudoa* pseudocyst counts (made on a total of 562 fish exclusive of fish under 27 cm) were analyzed on the NWAFC Burroughs 7800 computer system using the SPSS software package described by Nie et al. (1970) and SPSS Update 7-9 (Hull and Nie 1981).

Fitted regression curves between cooked texture values and white and black pseudocyst counts were drawn using robust locally weighted regression analyses described by Cleveland (1979). The method was used to smooth scatterplots by calculating a polynomial fit to data using weighted least squares.

RESULTS AND DISCUSSION

Relationship Between Sensory Texture Ratings and Shear Press Values

Since any nonsensory evaluations of a fishery product must ultimately relate to the products' intrinsic organoleptic properties, emphasis in this study was placed upon taste tests despite the inherent fatigue factor associated with testing large numbers of samples. No consumer-type panel was carried out to test the accuracy of the texture evaluation, because fish with abnormal

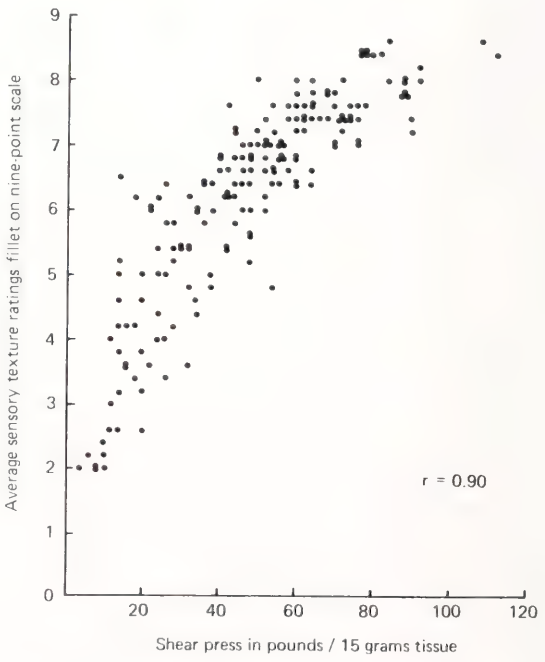

FIGURE 4.—Scatterplot and Spearman correlation coefficient (r) between sensory texture rating and shear press force of cooked flesh of Pacific whiting fillets.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]J. Wall, REFM Division, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., BIN C15700, Seattle, WA 98115, pers. commun. March 1985.

texture were purposely included in the present study to determine the extent of the problem. On randomly selected samples, shear press measurements were run concurrently as an objective support for the sensory data.

A scatterplot and the Spearman correlation coefficient (nonparametric) determined for the sensory texture ratings and shear press values shown in Figure 4 was produced by the SPSS software. The high degree of correlation ($r = 0.90$ at $P = 0.001$) was found to support the credibility of sensory texture evaluation in this study.

Effect of White and Black Pseudocysts and *Kudoa* Species Upon Sensory Texture

Fitted regression curves for sensory texture values and white pseudocyst counts are shown in Figure 5A. Mixed infections include both *K. paniformis* and *K. thyrsitis* pseudocysts in the same fish. The curve representing the white mixed infection shown superimposed on that of the white *K. paniformis* curve suggests that most of the white mixed pseudocysts consisted of *K. pani-*

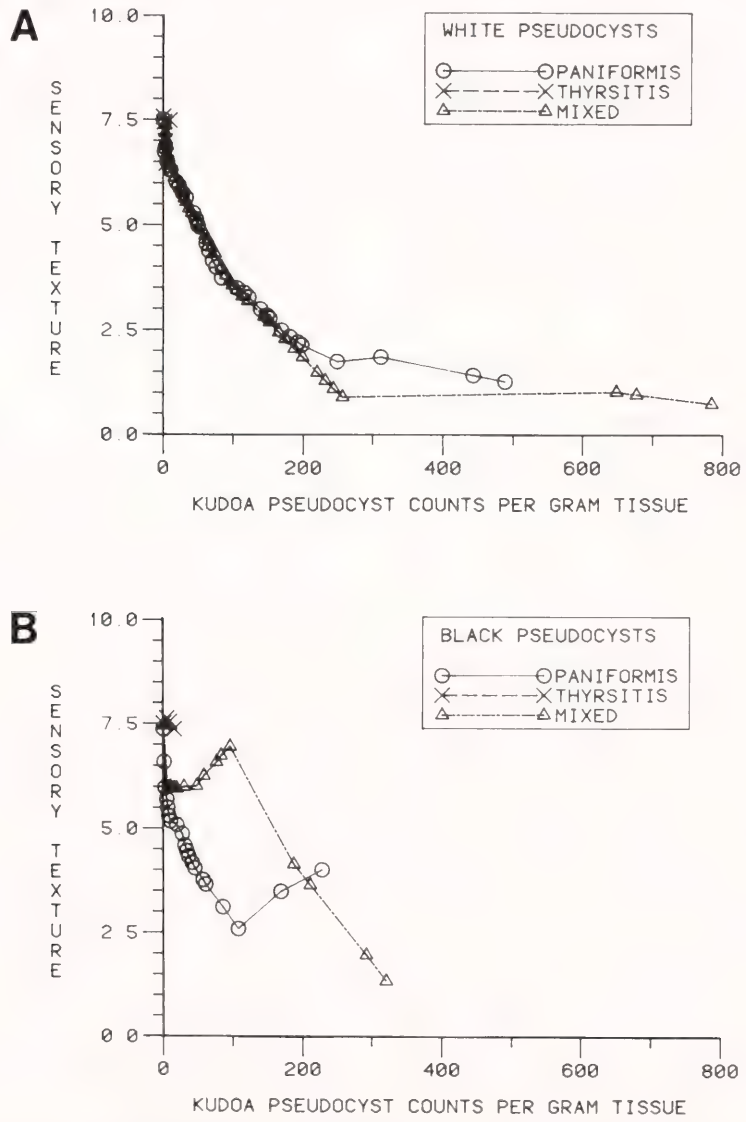

FIGURE 5.—Fitted regression curves between cooked texture of Pacific whiting and intensity of (A) white *Kudoa* pseudocysts and (B) black pseudocysts.

formis. Correlation values for these two curves were $r = -0.79$ and -0.80, respectively (Table 2). Pseudocyst counts of white *K. thyrsitis* were <10 and did not appear to adversely affect the texture of the Pacific whiting (Table 3A). The low count is thought by Kabata and Whitaker (1981) to be the result of an evolutionary development of defense mechanisms in the host fish. The correlation coefficient representing sensory textures and white *K. thyrsitis* infection was 0.12. This suggests that *K. thyrsitis* plays an insignificant role in the texture quality of Pacific whiting, a view also held by Kabata and Whitaker (1981).

Fitted regression curves between sensory textures and black pseudocyst counts are shown in Figure 5B. Mixed black pseudocyst counts did not follow the pattern for black *K. paniformis* counts, as observed with the white mixed and *K. paniformis* infections. This suggests that the black pseudocyst counts cannot be used as a reliable predictor of sensory texture. Magnitudes of black *K. paniformis* counts and black mixed counts were <320, while counts were <16 for black *K. thyrsitis*. Like those infected with white *K. thyrsitis*, fish infected with black *K. thyrsitis* parasites had normal, firm cooked textures (Table 3A). The absolute value of the Spearman correlation coefficient (Table 2) between texture quality and black pseudocyst intensity was lower (-0.38) than that of the coefficient for texture quality and white pseudocyst intensity (-0.74), both at significance level of 0.001.

From the correlation coefficients for the white and black pseudocyst counts of both species, the square of the coefficients (coefficient of determination) was calculated to compare their relative importance in terms of differences in their magnitude with respect to one another. Fifty-five percent of the observed variability in all sensory texture ratings can be accounted for (predicted) by the observed variability in the white pseudocyst counts, while only 14% can be accounted for by the observed variability in the black pseudocysts counts. However, infections do not occur in Pacific whiting as only white or black pseudocysts; they also occur as a mixture of the two. Thus, when the quantitative effects of the white or black pseudocyst counts on sensory texture were evaluated by multiple regression analysis, we found that only 1.5% of the variability in sensory texture rating was accounted for by black pseudocyst counts, and 45% accounted for by white pseudocyst counts. These figures represent partial coefficients of determination which indicate the relationship between two variables while controlling the effects of one or more other variables and are consistent with the findings of Patashnik et al. (1982) and Tsuyuki et al. (1982).

TABLE 2.—Spearman correlation coefficient between sensory texture rating and *Kudoa* pseudocysts in Pacific whiting caught during the summer of 1983.

Sensory texture with:	Sample size	Correlation coefficient	Significance
White pseudocysts			
total population	562	−0.74	0.001
Black pseudocysts			
total population	562	−0.38	0.001
K. paniformis			
white pseudocysts	201	−0.80	0.001
black pseudocysts	201	−0.66	0.001
K. thyrsitis			
white pseudocysts	191	−0.12	0.05
black pseudocysts	191	0.07	0.15
Mixed infection			
white pseudocysts	259	−0.79	0.001
black pseudocysts	259	−0.49	0.001

TABLE 3.—Percentage of sensory texture ratings for (A) each *Kudoa* species, (B) fork length, and (C) sex composition for Pacific whiting caught during the summer of 1983.

Description	Sample size	Sensory texture rating (%)			
		Normal	Soft	Abnormal	Total
(A) *Kudoa* species					
K. paniformis	144	17	5	3	26
K. thyrsitis	125	22	0	0	22
Mixed infection	190	23	7	4	34
None	103	18	0	0	18
Total	562	80	12	7	100
(B) Fork length composition of whiting					
Small (27-39 cm)	144	93	5	2	100
Medium (40-49 cm)	172	79	17	4	100
Medium large (50-59 cm)	170	74	14	12	100
Large (60-80 cm)	76	72	15	13	100
All lengths	562	80	13	7	100
(C) Sex composition of whiting					
Female	332	81	12	6	100
Male	227	79	13	8	100
Total	559	80	13	7	100

Intensity of White and Black Pseudocyst Infection in Relation to Sensory Texture Ratings

The magnitude of white and black pseudocyst counts in relation to their corresponding sensory texture scores are shown in Tables 4 and 5.

A total of 214 fish, 38% of the fish examined, did not have white pseudocysts. Table 4 shows that texture scores for this group of fish range from 4 to 9 with 97% of the scores in the range of

6 to 8. Fish infected with white pseudocysts to the degree of 26 to 50 counts (average for the six areas in each fish tested) resulted in 1 out of 50 fish tested with a sensory texture score of 2. Thus, 2% of the fish in this category must be regarded as too soft and are organoleptically unacceptable (Table 1). In the sample of 562 fish, 25 specimens were found with white pseudocyst counts ranging between 51 and 75, none of which were judged to have a texture score of 2 or lower. However, note that 11 of 25 (44%) fish samples were soft textured. When the white pseudocyst counts were 76 or higher, nearly all of the fish were soft or abnormally soft textured.

The frequency distribution of sensory texture scores vs. black pseudocyst counts (Table 5) does not show the same relationship that intensity of white pseudocyst infection had on sensory texture (Table 4). This becomes evident after examining sensory texture scores for fish with black pseudocyst counts of 1 to 25 (Table 5) when the entire range of texture scores is represented.

Note, however, that the observed distributions of white and black pseudocysts differ. For example, of the 98 fish with pseudocyst counts exceeding 50, 81 had white pseudocysts but only 17 had black pseudocysts. Also, for Pacific whiting with counts >100, 37 of 45 (82%) with white pseudo-

TABLE 4.—Frequency distribution of fish in each sensory texture score category and intensity of white pseudocyst infection in Pacific whiting over 27 cm. $n = 562$.

White pseudocyst count (ave./fillet)	Number of fish in each sensory texture score category									Row total	Percent of n
	9	8	7	6	5	4	3	2	1		
0	5	131	69	7	1	1				214	38.1
1-10	2	49	59	24	14	2	1			151	26.9
11-25	1	5	15	23	11	9	2			66	11.7
26-50		3	5	18	14	5	4	1		50	8.9
51-75			2	3	9	10	1	0		25	4.4
76-100			0	1	2	3	3	0	2	11	2.0
101-125		1	0	1	1	1	4	5	1	14	2.5
126-150						1	1	1	0	3	0.5
151-200						2	3	9	2	16	2.8
201-300							1	1	4	6	1.1
301-400						1	0	0	0	1	0.2
401-800								1	4	5	0.9
Total of infected fish	3	58	81	70	51	34	20	18	13	348	
Percent of n	0.5	10.3	14.4	12.5	9.1	6.0	3.6	3.2	2.3	61.9	100.0

TABLE 5.—Frequency distribution of fish in each sensory texture score category and intensity of black pseudocyst infection in Pacific whiting over 27 cm. $n = 562$.

Black pseudocyst count (ave./fillet)	Number of fish in each sensory texture score category									Row total	Percent of n
	9	8	7	6	5	4	3	2	1		
0	2	97	72	15	9	4	3	2	0	204	36.3
1-10	5	74	62	42	31	21	8	6	4	253	45.0
11-25	1	14	10	9	8	5	4	5	2	58	10.3
26-50		4	3	7	4	4	1	4	3	30	5.3
51-75			1	2	0	0	2	0	0	5	0.9
76-100			2	0	0	0	1	0	1	4	0.7
101-125					0	1	0	0	1	2	0.4
126-150					0	0	0	0	0	0	0
151-200				1	0	0	0	0	1	2	0.4
201-300				1	0	0	1	1	0	3	0.5
301-400									1	1	0.2
401-800										0	0
Total of infected fish	6	92	78	62	43	31	17	16	13	358	
Percent of n	1.1	16.4	13.9	11.0	7.7	5.5	3.0	2.8	2.3	63.7	100.0

cyst counts and 5 of 8 (63%) with black pseudocyst counts fell in the 1 to 3 texture category. Although the data are limited, this may suggest that for lower counts black pseudocysts are not related to poor texture, whereas for higher counts, they are ($r = -0.38$ at $P = 0.001$).

In this study, 459 out of 562 fish were infected with the myxosporean parasite *Kudoa*. However, knowing that only white pseudocysts contain the parasites that produce the proteolytic enzymes that adversely affect texture (Tsuyuki et al. 1982), the assessment of the effect of pseudocyst infections on texture was necessarily confined to white pseudocyst counts only. Therefore, in order to determine the most likely white pseudocyst count which, when exceeded, would produce an abnormal texture in the cooked fish, the following analysis was made. On the scale of firmness in Table 1, the minimum acceptable texture value was defined as 3. Only 20 fish were rated 3. Their mean intensity of infection was 94.9 pseudocyst counts and median intensity was 88. Consequently, fish with median intensity ≥88 pseudocyst counts were hypothesized to be abnormally textured. On a qualitative scale this level of infection was considered heavy. To test this hypothesis, all fish having infection intensities ≥88 white pseudocyst counts were computer selected. There were 50 such fish. These included 90.3% of all the fish with abnormal textures (sensory rating of 1 to 2), but also included 3.9% of all the normal or soft-textured fish (sensory rating of 3 to 9). Next, fish with average sensory textures (5) were selected to determine the white pseudocyst counts below which sensory textures would most likely be normal. The median pseudocyst count for these fish was 23. Counts below 23 were considered indications of a light infection. The level of infection between these two counts (23 to 88) was considered to be moderate.

Because black pseudocyst counts correlated poorly with sensory texture in this study, the degree of black pseudocyst infection had to be arrived at from cullability figures using the culling techniques described previously. The cullability categories were determined visually and, like the white pseudocysts, described as light, moderate, and heavy. Confidence limits for black pseudocyst counts for each cullability category were statistically determined and the midpoint between the high end of one confidence limit and the low end of the adjoining confidence limits was taken as the dividing point. The following range of black pseudocyst counts was arrived at for each category: none (0); light (1 to 28); moderate (29 to 79); heavy (80 or more).

Effect of Geographical Areas

Data in Figure 6A shows the percentage of the catch from the various survey areas sampled in this study and their related sensory textures. Based on results of our sensory evaluations, 13% of the Pacific whiting harvested from the Monterey-Eureka, CA, sampling areas had abnormal textures, whereas only 1 to 3% of the Pacific whiting caught between the Columbia River and Vancouver Island had abnormal textures. The correlation coefficient between survey area and sensory texture rating was 0.20 at $P = 0.001$.

Similarly, the incidence of heavy white pseudocyst infection (>88 pseudocyst counts) was about threefold greater in the Pacific whiting from the Monterey-Eureka, CA, corridor (Fig. 6B) than in whiting caught between the Columbia River and Vancouver Island, i.e., 16 to 11% vs. 5 to 4%. The percentage of no white pseudocyst found in the fish samples from all survey areas ranged from 25 to 34%.

The trend in black pseudocyst counts (Fig. 6C) was similar to the trend in white pseudocyst counts in that more heavy (>80) black pseudocyst counts were observed in Pacific whiting caught between Monterey-Eureka, CA, and the Columbia River than in Pacific whiting from the Vancouver Island area. Two to three percent of the Pacific whiting sampled from the area between Monterey, CA, and the Columbia River were heavily infected with black pseudocysts, whereas no heavy black pseudocyst infections were found in the Pacific whiting caught from Vancouver Island area. Infections of black pseudocysts in Pacific whiting from the Vancouver Island area were primarily light (1 to 29), the category into which 84% of the infected fish fell, and moderate infections (29 to 79), the category in which 4% of the infected fish fell.

Table 6A shows the prevalence of the *Kudoa* species found in Pacific whiting caught between Monterey, CA, and Vancouver Island, Canada. *Kudoa paniformis* was the predominant species (average 36 to 37%) found in the Pacific whiting taken in the Monterey-Eureka area, whereas *K. thyrsitis* was the predominant species (29 to 40%) in the fish caught north of the Columbia River. Mixed infections averaged 34% for the combined survey areas.

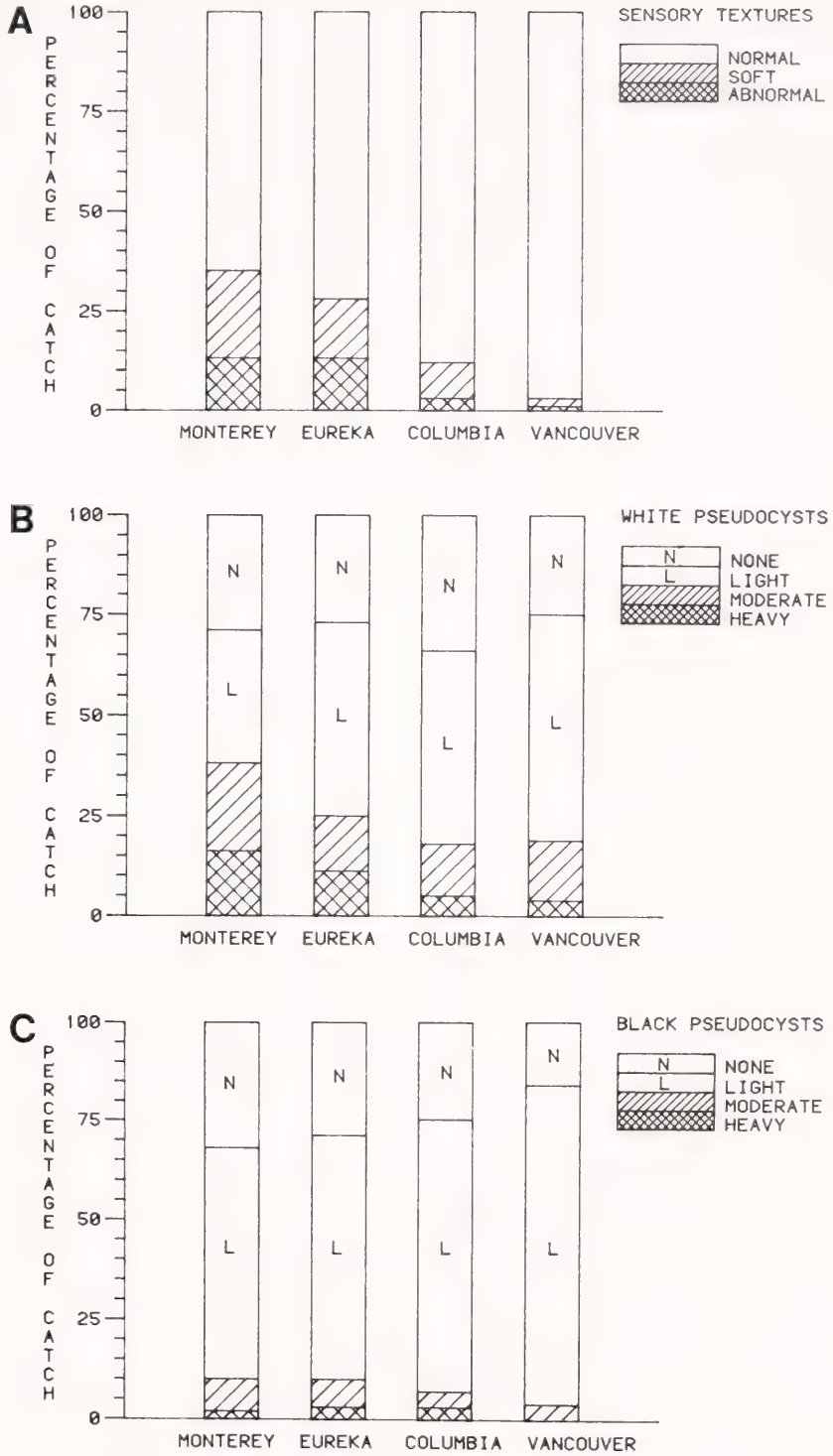

FIGURE 6.—Occurrence (%) of (A) sensory texture categories, (B) degree of white pseudocyst infection, and (C) degree of black pseudocyst infection of Pacific whiting, by INFPC areas.

TABLE 6.—(A) Prevalence of *Kudoa* species, (B) fork length composition (%), and (C) sex ratio of Pacific whiting samples in the INPFC catch survey area.

Description	INPFC survey area				
	Monterey	Eureka	Columbia	Vancouver	All areas
Sample size (fishes)	136	117	234	75	562
(A) *Kudoa* species (%)					
K. paniformis	36	37	18	15	26
K. thyrsitis	7	15	29	40	22
Mixed infection	35	27	35	39	34
None	22	21	19	7	18
(B) Fork length composition (%)					
Small (27-39 cm)	30	33	26	7	26
Medium (40-49 cm)	31	29	31	32	31
Medium large (50-59 cm)	27	28	30	40	30
Large (60-80 cm)	13	10	13	21	14
(C) Ratio of female/male	1.2	1.3	1.6	2.2	1.5

Effect of Biological Factors on Sensory Texture

Biological data showing sex composition, the ratio of females to males, and representative fork lengths (FL) and their relationship to corresponding sensory textures and survey areas are given in Tables 3B, 3C, 6B, and 6C, respectively. The ratio of females to males nearly doubled as fishing activities in this study moved from south to north along the Pacific coast. Concurrently, the fork length of the fish increased as well. About 60% of the largest fish (60 to 80 cm FL) were caught between the Columbia River and Vancouver Island. More abnormal textures were oberved in the larger fish than in the smaller fish (Table 3B). Based on the total number of specimens examined, however, the correlation coefficient for the relationship between fork length and sensory texture was low ($r = -0.21$ at $P = 0.001$).

Sensory texture was not found to be related to the sex of the fish ($r = 0.04$ at $P = 0.181$, Table 3C). The percentage of abnormal textures in the female and male fish was about the same, i.e., 6 and 8%, respectively, confirming the reports of Kabata and Whitaker (1981). Similarly, males and females were evenly distributed (approximately 12%) in the soft-texture category.

The Relationship of Pseudocyst Counts to Location of Infection in a Fillet Area to Texture

Results of analyses to determine the relationship of intensity of infection in a fillet area (Fig. 3) to texture quality are shown in Table 7. Pseudocyst infections were found throughout the fillet areas. The highest percentage (11 to 12%) of heavy infections of white pseudocysts were located in the nape area, whereas the lowest incidence (8%) was located in the tail ($r = 0.89$ at

TABLE 7.—Percentage of degree of *Kudoa* pseudocyst infection and corresponding sensory textures found in preselected examination areas of Pacific whiting fillets.

	Fillet area examined					
	Nape		Middle		Tail	
	Dorsal	Ventral	Dorsal	Ventral	Dorsal	Ventral
Degree of white pseudocyst infection (%)/examination area						
None	38	41	41	43	46	46
Light (1-22)[1]	32	34	33	37	32	34
Moderate (23-87)[1]	18	15	17	13	15	13
Heavy (88 and over)[1]	12	11	9	8	8	8
Degree of black pseudocyst infection (%)/examination area						
None	41	34	43	40	44	41
Light (1-28)[1]	51	55	51	52	50	54
Moderate (29-79)[1]	6	8	4	6	5	3
Heavy (80 and over)[1]	2	3	2	2	1	2
Sensory texture(s) (%)/examination area						
Normal	77	82	81	85	85	87
Soft	12	10	11	10	10	10
Abnormal	11	8	8	5	5	4
Sample size	502	548	562	556	560	551

[1]Pseudocyst counts.

$P = 0.008$). Incidences of heavy infections of black pseudocysts were 2 to 3% at the nape and about 1 to 2% at the tail ($r = 0.71$ at $P = 0.06$). In general, there tend to be more black and/or white pseudocysts in the nape than in the tail area, although the correlation of white pseudocysts in the dorsal to ventral direction was rather low ($r = -0.21$ at $P = 0.035$).

Sensory texture profiles shown in Table 7 indicated that more abnormal textures were found in the nape area (11 to 8%) than in the tail area (5 to 4%) of the fish examined ($r = 0.48$ at $P = 0.16$).

Effect of Culling

At the present time, there is no accepted method or methods for efficiently detecting and culling Pacific whiting infected with white or black pseudocysts. Ultraviolet light and back lighting with white light have been tried on occasion, but these techniques have not been developed enough to be effective for use in Pacific whiting production. This leaves visual detection as the only on-site method for detecting and removing suspect Pacific whiting from the production line. However, as there are no reliable data available concerning the effectiveness of visual culling, an attempt was made in this study to estimate its potential usefulness.

Criteria for culling (Patashnik et al. 1982) in this study was described in a previous section. Of the 562 fish examined, 34 were visually culled on the basis of a moderate to heavy degree of white and black pseudocyst infection. Of these, 10 fillets were moderately to heavily infected with white pseudocysts, 7 with both black and white pseudocysts, and 17 with only black pseudocysts. Based on the criteria developed by Patashnik et al. (1982), these results suggest that culling fillets that are moderately or heavily infected with pseudocysts appears possible. However, since culling has not been successfully demonstrated in a commercial setting, the technique may prove to be too difficult and time consuming to be practical.

CONCLUSIONS

Overall, 18% of the Pacific whiting samples collected for this study were uninfected with *Kudoa*. Furthermore 65% had counts of <10 white pseudocysts, and only 10% had counts over 100 white pseudocysts. By comparison, 81% of the fish samples had <10 black pseudocysts counted and only 1% were infected with over 100 black pseudocysts counted.

When both the white and black pseudocyst counts were considered collectively, the variation in white pseudocysts explained 55% of the variation in sensory texture, whereas black pseudocysts accounted for 14%. However, when the effect of the white pseudocysts was mathematically removed from the fish samples having both, the black pseudocysts were found to explain only 1.5% of the variation in sensory texture.

Infections of white *K. paniformis* and white mixed infections correlated ($r = 0.80$ and 0.79, respectively) with the variations in sensory texture better than the black *K. paniformis* or black mixed infections (0.66 and 0.49, respectively). Neither the white nor the black *K. thyrsitis* pseudocyst counts correlated well with sensory textures. Although common in the Pacific whiting samples examined in this study, *K. thyrsitis* consistently were found in low numbers. On the other hand, *K. paniformis* were identified in 26% of the sample, and mixed infections were observed in 34% of the fish examined.

The heaviest infections of white and black *Kudoa* sp. pseudocysts were found in the Pacific whiting caught off the coast of California. The highest percentage of abnormal sensory textures were also observed in the fish harvested off the California coast.

Generally, in this study, we found that the larger the fish the greater the incidence of abnormal textures. Sex of the fish had no apparent effect on the quality of sensory texture.

Anatomically, the nape and dorsal areas of the Pacific whiting samples examined tended to have higher counts of white pseudocysts, and therefore more abnormal textures, than the other areas of the fish examined. The occurrence of heavy white pseudocyst infections in the nape, middle, and tail sections of the fish samples averaged 11.5%, 8.5%, and 8%, respectively. Heavy black pseudocyst infections were 2.5%, 2%, and 1.5% for nape, middle, and tail sections. Overall, abnormal textures were found 9.5% of the time in the nape, 6.5% in the middle, and 4.5% in the tail. Differences in the number of white pseudocyst counts found between the dorsal and ventral sides of the fish were small. The occurrence of abnormal texture was 30% greater for the dorsal side of the fish than the ventral side.

Results of visual culling in this study suggest that the method may have some potential, but

that the technique has yet to be successfully demonstrated under commercial conditions.

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DISTRIBUTION AND ABUNDANCE OF BILLFISH LARVAE (PISCES: ISTIOPHORIDAE) IN THE GREAT BARRIER REEF LAGOON AND CORAL SEA NEAR LIZARD ISLAND, AUSTRALIA

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ABSTRACT

Istiophorid larvae were relatively common in plankton samples from the Lizard Island region in November to early March 1980-85. Black marlin, blue marlin, and sailfish larvae were captured. Larvae of all three taxa were most concentrated and abundant in the Coral Sea immediately seaward (= windward) of the outer ribbon reefs. Concentration and abundance within the Great Barrier Reef Lagoon were not usually different from those more than 0.25 nautical miles offshore in the Coral Sea. Size-frequency data combined with the distributional information suggest that spawning or at least hatching of eggs was concentrated in the area within 0.25 nautical mile seaward of the reef crest. Preflexion larvae of blue marlin and sailfish were essentially confined to the upper 6 m of the water column (and perhaps the upper half of that), but not the neuston. Preflexion larvae of all three species dominated the oblique bongo net tows (98%), while postflexion larvae dominated the neuston samples (76%). This suggests an upward ontogenetic movement.

The horizontal distribution of istiophorid larvae is probably the result of spawning close to the reef front, an area of supposed downwelling, combined with the proclivity of the larvae to occupy surface waters. This should lead to retention of larvae in the forereef area. Some caveats about accepting this hypothesis as a complete explanation for the horizontal distribution of istiophorid larvae are discussed.

Near-reef areas appear to be important in the early life history of istiophorids at least in the Coral Sea and for the three taxa studied.

The billfishes of the family Istiophoridae are large, high trophic level, pelagic fishes of considerable sport and commercial importance throughout tropical and subtropical oceans (Nakamura 1985). Information on their early life history is limited and investigations have been hampered by the relative rarity of the larvae. Studies on the distribution of istiophorid larvae in the Indo-Pacific have dealt with distributions over very broad areas and have not examined distributions on a small scale, particularly those very close to reefs. (The considerable Japanese work was summarized by Nishikawa et al. 1985 and the Russian work by Gorbunova 1976.) Size of larvae in relation to horizontal distribution has only rarely been considered. Aside from reports that istiophorid larvae had been captured in neuston tows (e.g., Bartlett and Haedrich 1968; Gorbunova 1976) the only published information on vertical distribution of istiophorid larvae was provided by Ueyanagi (1964), who concluded billfish larvae were largely confined to surface waters during the day and dispersed through the upper 50 m at night.

During studies on the distributional ecology of the larvae of reef fishes in the vicinity of Lizard Island in the northern region of the Great Barrier Reef, Australia, two of us (Leis and Goldman) have sampled extensively in the Great Barrier Reef Lagoon and the near-reef waters of the Coral Sea. In our samples, we captured a relatively large number of istiophorid larvae. This has provided information which sheds light on little known aspects of the early life history of istiophorids and in view of the widespread interest in istiophorid biology, we have prepared this summary on the horizontal and vertical distribution of istiophorid larvae over relatively small scales and how these relate to development of the larvae. Because istiophorid larvae are difficult to identify, we have collaborated to insure accuracy in identification of the larvae.

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MATERIALS AND METHODS

All samples considered here were taken in an area between Lizard Island, approximately midway across the Great Barrier Reef Lagoon, to 10 nmi seaward of the outer ribbon reefs of the Great Barrier Reef in the Coral Sea (Fig. 1).

The Great Barrier Reef Lagoon is modally 30 m deep in this region (range 25-40 m). The outer ribbon reefs are located along the shelf break, and the bottom falls off sharply with distance into the Coral Sea reaching depths >2,000 m within 6 nmi (Fig. 1).

The samples immediately to windward of Lizard Island were taken from a 7 m boat with a net of 0.4 m^2 mouth area (see Leis 1986 for further details of sampling). Other samples were taken from RV *Sunbird*, a 14 m catamaran. The neuston net, with mouth dimensions of 1 × 0.3 m and 0.5 mm mesh, was towed between the bows of the catamaran, and normally fished to a depth of 0.1 m. Bongo nets of 0.85 m diameter and fitted with a depressor were towed in a double-oblique pattern to study horizontal distribution or in opening-closing mode to study vertical distribution. Nets were towed at approximately 1 m/second, were of 0.5 mm mesh, and were equipped with a flowmeter. During the vertical distribution study, a depth sensor with a deck display was fitted to the net. At other times, a mechanical depth-distance recorder was used.

The neuston net, when used, fished during the bongo net tow. The oblique bongo net tows were done to the greatest calculated depth that was

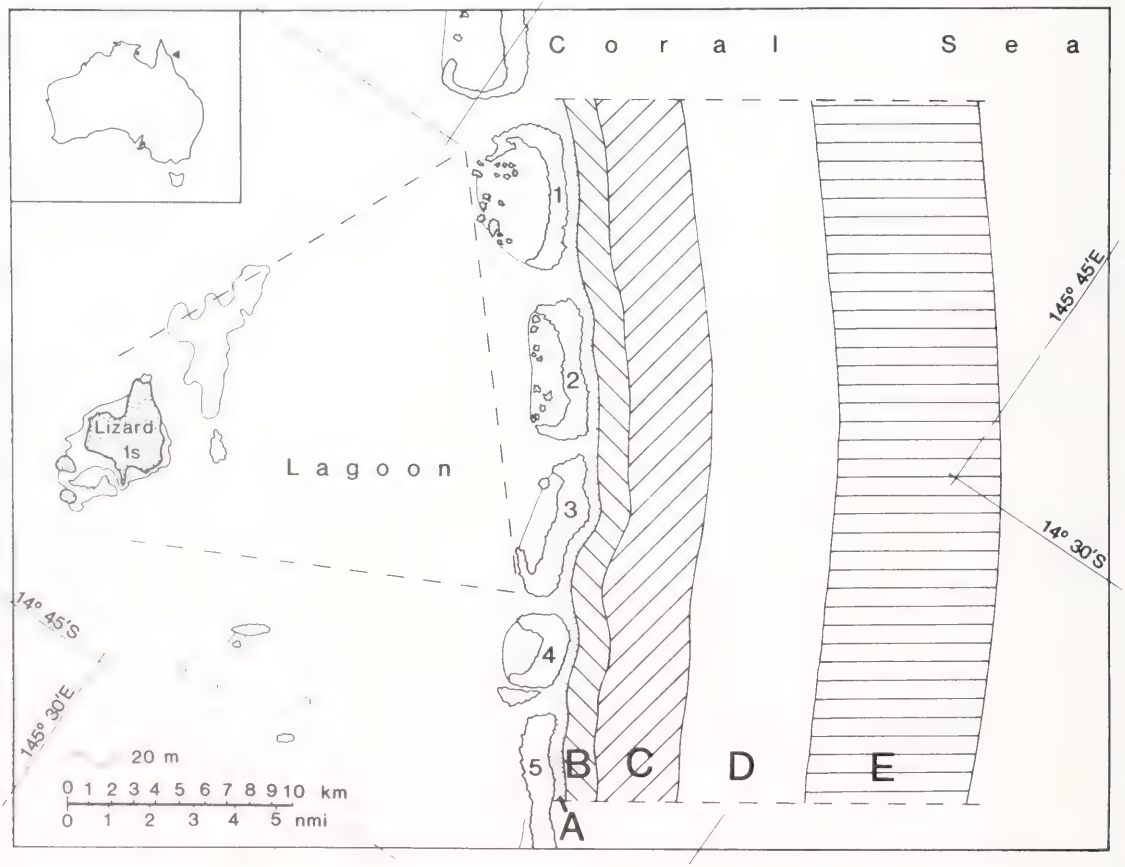

FIGURE 1.—Map of the study area. One sampling block is the Great Barrier Reef Lagoon beween Lizard Island and the ribbon reefs, this is delineated by the broken lines. In the Coral Sea, there are five sampling blocks A-E as defined in the text. Depths in the Lagoon range from 20 to 40 m. Depths to 400 m are encountered in Coral Sea block A, to 1,000 m in block B and >1,500 m in C-E. Outer ribbon reefs are 1) Day, 2) Carter, 3) Yonge, 4) No Name, and 5) Number 10 Ribbon. None of the outer reefs are emergent.

considered safe in the lagoon and close to the windward face of the reef. Because of the great variations in bottom topography in the latter area, the net actually hit bottom upon occasion. Further offshore, bongo net tows were done with a standard amount of wire out which ensured a maximum sampling depth in excess of 100 m.

Position fixing in the Coral Sea was by radar reflection of the waves breaking on the reef crest when close to the reef. This meant that actual distance off the reef varied somewhat (~100 m) depending on sea state and tide. Four cruises were made to investigate horizontal distribution: 1) 2-5 November 1984, 2) 17 and 20-22 November 1984, 3) 30 January-2 February 1985, and 4) 9-13 February 1985. On each cruise, six samples were taken between Lizard Island and the outer reef on one day (Fig. 1), and three days were spent in the Coral Sea running a transect each day and starting at opposite ends of the transect on alternate days. On each transect, two randomly located samples were taken in each of five offshore blocks defined by distance (nmi) from the outer reef crest (Fig. 1): A, 0-0.25 nmi; B, 0.25-1.0 nmi; C, 1.0-3.0 nmi; D, 3.0-6.0 nmi; E, 6.0-10.0 nmi. Therefore, six samples were taken in each block on each cruise. The three transects on a cruise were each centered off a different reef (i.e., either of Day, Carter, Yonge, No Name, or Number 10 Ribbon Reefs). Bad weather and high volumes of floating pumice precluded the routine use of the neuston net. There were some variations in this plan owing to weather or equipment problems, the most serious of which was missing 4 of 6 samples in block A on the second cruise. Larvae from other samples taken with similar methods in November 1983 were also included where appropriate. Funding limitations prevented processing of samples from block D.

The vertical distribution samples were taken in the lee of Carter Reef primarily in the Great Barrier Reef Lagoon, but partially in the pass to the north of Carter Reef (Fig. 1). Samples were taken in sets; each set consisted of a neuston tow and 3 bongo net (0-6 m, 6-13 m, and 13-20 m) tows. The 0-6 m stratum was sampled in the undisturbed water flowing between the hulls of the catamaran. In February-March 1983, 22 such sets were taken, 8 each in morning and afternoon and 6 at night.

Additional samples from within the Great Barrier Reef Lagoon as reported by Leis and Goldman (1984, 1987) and Leis (1986) were used for seasonality information. Samples in the Lagoon were taken in all months but May, June, August, September, and December. Samples were taken in the Coral Sea in October, November, January, and February.

Oblique bongo net tows typically filtered 1,000-1,500 m^3 and horizontally stratified tows filtered 400 m^3. Neuston tows typically travelled 1,200-2,000 m. All nets were carefully washed after each tow and the sample preserved in 5-10% seawater-formalin.

In the laboratory, samples were sorted using a dissection microscope (~10×) and all larvae removed. Samples from both sides of the bongo net were fully sorted except for the Great Barrier Reef Lagoon samples from February-March 1983 and November 1984 when only side was sorted because of high plankton volume. Larvae were placed in 70% ethanol prior to measurement. Identification of larvae followed Ueyangi (1963, 1974a, b). Larvae were measured using an eyepiece micrometer of a dissection microscope to the nearest 0.1 mm. Notochord length and standard length were measured for preflexion and postflexion larvae, respectively (Leis and Rennis 1983). Larvae from these samples are deposited in the Australian Museum, Sydney.

Numbers of larvae per sample were converted to numbers per volume (concentration) and numbers per area (abundance) using standard methods (Leis 1986). In analysis of vertical distribution data, only positive sets (i.e., those in which at least one larva was captured) were considered. Statistical methods followed Conover (1971) and Zar (1974). References to the Student-Newman-Keuls (SNK) test refer to the version based on ranks (Zar 1974).

RESULTS

Identification

We captured larvae of black marlin, *Makaira indica*; blue marlin, *Makaira mazara*; striped marlin, *Tetrapturus audax*; and Indo-Pacific sailfish, *Istiophorus platypterus*. The larvae here identified as black marlin correspond to the "non-pigmented" sailfish of Ueyanagi (1974a, b). This type of istiophorid larva has been captured only in the seas off northern Australia and the southern portion of the Indonesia-New Guinea archipelago (Ueyanagi 1974a, b). In our Coral Sea samples these larvae were found almost exclusively during November, the time when large

numbers of gravid female black marlin occur in the area (B. Goldman pers. obs.; J. Pepperell[4]). A major sport fishery is based on this apparent spawning migration and the catches are made primarily just off the windward reef faces in the northern Coral Sea. When sampling in November 1984, our research vessel was frequently operating in the midst of the sport fishing fleet. This circumstantial evidence suggested the possibility that the "non-pigmented" sailfish larva was in fact the larva of the black marlin, and led us to recheck these "non-pigmented" sailfish larvae. Two specimens (5.6 and 9.7 mm) were cleared and stained for bone and cartilage (Potthoff 1984); both specimens had vertebral formulae of 11+13=24. This confirms that they are of the genus *Makaira* (Nakamura 1985). These larvae can be distinguished from those of the only other Indo-Pacific member of the genus, the blue marlin, by head profile and depth and minor pigment differences. Therefore, we concluded that the "non-pigmented" sailfish larva captured in the present study were black marlin. A more detailed treatment of the identity of "non-pigmented" sailfish larvae will be given separately (Ueyanagi and Leis in prep.).

The larvae identified here as sailfish are normally pigmented sailfish larvae which had not previously been reported from the Coral Sea (Ueyanagi 1974a, b). Only a few striped marlin larvae were captured, and because nearly all were small and only tentatively identified, they are not considered further.

Seasonal Occurrence

Sailfish larvae were taken only in January, February, and March. Blue marlin larvae were taken in mid-November, January, February, March, and April, although only one larva was taken in April. Black marlin larvae were taken throughout November, and three were taken in January-February.

A sequence of occurrence of larvae and presumably of spawning in the area begins with the appearance of black marlin larvae in late spring-early summer, followed by blue marlin in summer-autumn, and finally sailfish in late summer-early autumn.

Horizontal Distribution

Black marlin larvae were most concentrated in block A adjacent to the seaward side of the reef on all cruises (Table 1). Concentrations elsewhere were low, with median values usually of zero. However, data from only one cruise could be tested statistically. The distribution of abundance was similar to that of concentration, with the exception that abundance in the two near-reef blocks could not be shown to be significantly different during the first cruise. During the first two (November) cruises, black marlin larvae were taken in 7 of 8 samples from the near-reef area (block A). Only three black marlin larvae were taken on cruises three and four (January-February), all in block A. Black marlin larvae were present in only 13 of 96 samples taken elsewhere, and of these areas, block B (0.25-1.0 nmi offshore) had the highest frequency of occurrence, 5 of 24 samples.

Clearly, black marlin larvae were consistently found in greatest numbers closest to the seaward side of the reef. The offshore extent of this high density zone of black marlin larvae was very limited, extending at most to 1 nmi seaward (block B) of the reef crest, but more likely to only 0.25 nmi.

Blue marlin larvae were less abundant than black marlin in our samples but had a similar distributional pattern. Again, data from only one cruise (the third) could be tested statistically. Except for the second cruise, blue marlin larvae were both most concentrated and abundant in block A, the area closest to the seaward face of the reef (Table 1). Further, 8 of the 13 occurrences were in this block. During the second cruise, blue marlin larvae seemed most concentrated and abundant at block B (0.25-1.0 nmi off), but only six larvae were captured on this cruise and only two samples were taken in block A so the significance of these results is questionable. Blue marlin were, with the possible exception of the second cruise, consistently found in greatest numbers closest to the seaward side of the reef. This is similar to the pattern for black marlin. However, small numbers of blue marlin larvae were captured in block E, the most offshore segment of the transect, and this offshore area had the second highest frequency of occurrence of blue marlin larvae (Table 1).

Only 13 sailfish larvae were taken, and the data are too sparse to indicate much more than all but 1 of the 7 occurrences were in the two blocks nearest the reef front (A and B). Sailfish larvae

[4]J. Pepperell, Fisheries Research Institute, N.S.W. Department of Agriculture, Cronulla, N.S.W., Australia, pers. commun. 1986.

TABLE 1.—Distribution of istiophorid larvae based on transects from the Great Barrier Reef Lagoon into the Coral Sea. Co, concentration (larvae/1,000 m^3); Ab, abundance (larvae/100 m^2); f, frequency (i.e., number of positive hauls). Values for Co and Ab are medians, and parenthetically, ranges. P is for Kruskal-Wallis test. For tested data sets, values with the same superscript symbol (# or †) are not significantly different ($P > 0.05$, SNK Test). NT, not tested statistically: T, because only 2 samples were taken in block A; F, because too few larvae were taken. Normally, 6 samples were taken in each block on each cruise. No larvae were taken on the cruises not listed.

		Coral Sea blocks				
	Great Barrier Reef Lagoon	A (0-0.25 nmi)	B (0.25-1.0 nmi)	C (1.0-3.0 nmi)	E (6.0-10.0 nmi)	P
Black marlin						
1st cruise						
Co	0 (0-4.4)#	3.8 (0-11.3)	0.8 (0-1.9)#	0 (0-1.9)#	0 (0-0.5)#	0.04
Ab	0 (0-10.9)#	15.0 (0-56.5)†	10.5 (0-33.0)#†	0 (0-47.1)#	0 (0-13.0)#	0.06
f	1	5	4	2	2	
2d cruise						
Co	0 (0-1.4)	2.8 (1.1-4.5)	0 (0-0.5)	0 (0-1.2)	0	NT, T
Ab	0 (0-3.4)	12.8 (5.1-20.4)	0 (0-6.9)	0 (0-14.9)	0	
f	2	2 (of 2)	1	1	0	
3d cruise						
Co	0	0 (0-0.7)	0	0	0	NT, F
Ab	0	0 (0-2.0)	0	0	0	
f	0	2	0	0	0	
4th cruise						
Co	0	0 (0-1.2)	0	0	0	NT, F
Ab	0	0 (0-1.8)	0	0	0	
f	0	1	0	0	0	
Blue marlin						
2d cruise						
Co	0	0	0 (0-2.2)	0 (0-0.6)	0	NT, T, F
Ab	0	0	0 (0-23.0)	0 (0-7.2)	0	
f	0	0 (of 2)	2	1	0	
3d cruise						
Co	0#	1.5 (0-8.4)	0 (0-0.5)#	0#	0 (0-0.6)#	0.02
Ab	0#	12.6 (0-25.2)	0 (0-5.2)#	0#	0 (0-7.0)#	0.02
f	0	5	1	0	2	
4th cruise						
Co	0	0.33 (0-2.4)	0	0	0 (0-1.8)	NT, F
Ab	0	1.0 (0-7.7)	0	0	0 (0-21.1)	
f	0	3	0	0	2	
Sailfish						
3d cruise						
Co	0	0 (0-4.2)	0 (0-0.6)	0	0	NT, F
Ab	0	0 (0-12.6)	0 (0-6.1)	0	0	
f	0	1	2	0	0	
4th cruise						
Co	0	0 (0-2.6)	0 (0-0.8)	0 (0-0.7)	0	NT, F
Ab	0	0 (0-10.4)	0 (0-9.3)	0 (0-7.8)	0	
f	0	2	1	1	0	

may have a distribution similar to that of blue marlin and black marlin larvae (Table 1).

Sizes of Larvae From Bongo Net Tows

Black marlin larvae ranged from 2.5 to 6.8 mm with a strong mode at 2.8-2.9 mm (Table 2a). Statistical comparison of the size-frequency data between areas could only be undertaken for the first cruise. Data from block A were compared with data from all other areas pooled. The size-frequency distributions were possibly different (Kolmogorov-Smirnov test, $P = 0.07$): a greater proportion of the larvae were of the smaller size classes (<4 mm) in block A than in the other blocks. Inspection of the limited size-frequency data from the other cruises indicates a similar situation. More than one cohort of larvae was present because larvae on the second cruise were not larger than those on the first.

Blue marlin larvae ranged from 2.5 to 8.3 mm with a weak mode at 3.1 mm (Table 2b). Too few blue marlin larvae were captured to allow rigorous analysis of the size-frequency data, but there did not appear to be any difference in the size

TABLE 2.—Size frequency of a) black and b) blue marlin and c) sailfish larvae. If a block or cruise is not listed, no larvae were taken there. X indicates a hiatus in the size sequence. A few larvae too badly damaged to be measured were omitted. Blanks indicate zero.

a. Black marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	X	5.6	5.7	5.8	5.9	6.0	X	6.8
E	1st		1 1												
C	1st		1 1 1			1									
	2d		1 1												
B	1st		1 1 1 1			1	1					1			1
	2d		1 1												
A	1st	3 2 8 6	4 3 2 1 3	4 3 1		1 1			1		1				
	2d	1 3 1 2 3													
	3d	1													
	4th	1	1												
Lagoon	1st			1 1			1								
	2d	1	1												

b. Blue marlin

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0	4.5	5.0	5.5	X	8.3
E	3d	2								
	4th	1			1 1 1					1
C	2d		1							
B	2d	1 1 1				1				
	3d			1						
A	3d	2 1 1	4 2 1 2	1 1	1 1	1	1			
	4th		1		1		1	2		

c. Sailfish

Block	Cruise	Size class (mm) 2.5	3.0	3.5	4.0
C	4th			1	
B	3d		1 1		
	4th		1		
A	3d	2 3	1		
	4th	1 1	1		

composition of the larvae between areas. Larvae on the fourth cruise were apparently larger than those on the third, however it is doubtful that only one cohort was involved because of the small size difference between the two cruises which were about 10 days apart (Table 2b).

Sailfish larvae ranged from 2.5 to 3.8 mm, with a mode at 2.6 mm (Table 2c). Only 12 larvae were captured, but there is a suggestion that smaller larvae were taken nearest the windward reef face, and that the size of larvae increased with distance into the Coral Sea.

Vertical Distribution

Our information on vertical distribution comes primarily from samples taken within the Great Barrier Reef Lagoon. It is limited, but it is consistent.

In the sampling with opening-closing bongo net and neuston net, larvae of two species, sailfish and blue marlin, were captured. No istiophorid larvae were present in the neuston tows of the vertical distribution sets. Sailfish larvae were captured in 7 of 16 day-time vertical sets and none of the 6 night-time sets. All the sailfish larvae were captured in the 0-6 m stratum with the exception of two larvae, one from each of the two deeper strata, which came from two sets taken in one of the turbulent interreef channels during a falling tide (Table 3). Even with the inclusion of the data from the interreef channel, sailfish larvae were most concentrated in the 0-6 m stratum while concentrations in the other strata did not differ (Friedman test, SNK test, $P < 0.05$). Blue marlin larvae were captured in only three of the day-time vertical sets. All the blue marlin larvae were captured in the 0-6 m stratum, with the

TABLE 3.—Day-time vertical distribution of sailfish and blue marlin larvae in the vicinity of Carter Reef in February and March 1983. *N* refers to number of vertical sets (i.e., a tow in each stratum) that contained at least one larva of that species.

Sailfish ($N = 7$)

Depth stratum	Concentration (larvae/400 m^3)		Number of positive hauls (of 7)
	Median	Range	
Neuston	0	0-0	0
Bongo net			
0-6 m	1.7	0-7.8	6
6-13 m	0	0-1.6	1
13-20 m	0	0-1.0	1

Blue marlin ($N = 3$)

Depth stratum	Concentration (larvae/400 m^3)		Number of positive hauls (of 3)
	Median	Range	
Neuston	0	0-0	0
Bongo net			
0-6 m	1.8	1.8-4.3	3
6-13 m	0	0-0	0
13-20 m	0	0-1.0	1

exception of a single larva from 13 to 20 m from one of the interreef channel sets. In the three positive sets, blue marlin larvae were always most concentrated in the 0-6 m stratum, but there were too few data for rigorous testing.

Blue marlin and sailfish larvae occurred in one vertical set taken on the windward side of Lizard Island in January 1980 (see Leis 1986). One larva of each species was taken in each of the 0-1 m and the 3-4 m tows, while none were taken in the 6-7 m tow.

Istiophorid larvae from our neuston samples were developmentally more advanced (older) than those from bongo net samples. In all our samples, the bongo net captured 160 istiophorid larvae (black marlin, blue marlin, sailfish), three of which were postflexion stage, while the neuston net captured 17 istiophorid larvae (black marlin and blue marlin), 13 of which were postflexion stage (chi square, $P < 0.001$).

During the day preflexion blue marlin and sailfish larvae inhabit the upper 6 m, and possibly the upper half of that, but not the neuston. It appears that once the caudal fin is formed, istiophorid larvae move upward even more and enter the neuston.

DISCUSSION

Distribution of istiophorid larvae over such a small scale has not been studied previously, nor have such high concentrations of larvae been reported. Our results were surprising. Highest concentrations and abundances of istiophorid larvae in our study area were consistently found in the Coral Sea very close to the windward side of the ribbon reefs at the outer edge of the Great Barrier Reef. The size-frequency data (see below) suggest that this near-reef environment was a spawning area or just down wind of one for the three types of billfishes considered here.

Concentration and abundance of istiophorid larvae in the Great Barrier Reef Lagoon (hereafter referred to as the Lagoon) were always lower than in block A when both areas were sampled, but lagoonal numbers were generally not different from those further offshore in the Coral Sea. We cannot exclude the possibility that some istiophorid spawning takes place within the Lagoon, but believe it is more likely that the larvae were advected into the Lagoon through the interreef channels, as are larvae of many other oceanic fishes (Leis 1986; Leis and Goldman 1987). Still, concentrations of istiophorid larvae were high at times in the Lagoon (e.g., February-March 1983), and the relative survival of the larvae in the Lagoon vs. the Coral Sea is an open question.

The marginally significant difference between areas in size frequency of black marlin larvae suggests that hatching of the eggs takes place very near the windward face of the reefs. This also suggests that black marlin larvae found elsewhere were largely the result of dispersal away from the near-reef area, and these dispersed larvae had grown somewhat during their dispersal. Spawning could either be concentrated in the near-reef area or more widely spread, in which case the eggs would have become concentrated in the near-reef area through wind-induced surface drift and forereef downwelling (see below). Alternatively, larval growth rates could be higher or mortality lower in the areas further from the reef. Our data do not allow us to distinguish between these alternatives, but we believe the first is the most likely.

The data on blue marlin larvae gave no indication of differences in size frequency between areas. The lack of difference in size-frequency distribution could indicate that spawning in blue marlin was more evenly spread than in black marlin. If so, the increase in numbers nearest the windward side of the reef would be attributable to concentration and retention of larvae there. We cannot differentiate between this possibility and

the alternative that spawning is most intense near the reef.

Too few sailfish larvae were taken to make any firm statements on distribution of larvae of different sizes. However, they appeared to have a pattern of size distribution with location similar to that of black marlin larvae.

The vertical distribution data show that, at least during the day, preflexion larvae of blue marlin and sailfish concentrate in the upper few meters (perhaps upper 3 m) of the water column, but not in the neuston. However, postflexion larvae of blue marlin and black marlin are neustonic. This ontogenetic vertical migration has not been noted previously. The somewhat different results from the limited interreef channel samples could have been caused by turbulence due to strong tidal currents in these narrow passes.

Using nonclosing nets, Ueyanagi (1964) studied vertical distribution of istiophorid larvae (all taxa combined) over the upper 50 m and concluded that during the day larvae were most often caught at the surface and frequency of capture decreased with depth. At night catches of larvae were approximately evenly distributed over the upper 50 m. More recent data (Ueyanagi unpubl. data) confirmed this pattern for blue marlin, striped marlin, spearfish, and sailfish larvae.

It is possible that the observed horizontal distribution of istiophorid larvae in the Lizard Island area results solely from a concentration of spawning or at least hatching of eggs close to the windward side of the reefs. However, it is likely that additional factors are involved. The southeast trade winds push surface water against the windward sides of these reefs and although some of the water flows across the reefs into the Lagoon, downwelling (anstau conditions) should occur seaward of the reef. An organism which maintains a position near the top of the water column, as do the istiophorid larvae (or positively bouyant fish eggs), would accumulate in such a downwelling zone. A similar situation has been described off the windward reef at Lizard Island where larvae of a number of reef fishes with shallow-living larvae were apparently retained (Leis 1986). However, the istiophorid larvae apparently disperse away from the surface at night (Ueyanagi 1964) whereas the larvae retained off windward Lizard Island tended to maintain their day-time vertical distribution at night (Leis 1986). If they did leave the surface, the istiophorids might be advected away from the reef front. A further caveat against accepting the "anstau hypothesis" as a full and simple explanation for the distribution of istiophorid larvae in the area involves the trade winds. During the time the near-reef peak in istiophorid larvae was best developed (2-5 November), the winds varied from 0 to 10 kt and from northeast to southeast while on the other cruises, the wind was stronger and varied from 10 to 30 kt and from east to southeast. Finally, preliminary analysis of data from the samples in which the istiophorids were captured revealed that high abundances of a number of reef fish larvae also occur off the windward reef face. Many of these were not near-surface dwelling larvae. Further study of larval fish distributions and their causes in this area is clearly required.

Whatever the causes for the distributions of the istiophorid larvae very near the windward reef face, it is somewhat surprising that the larvae of epipelagic, oceanic fishes should be so abundant in such a narrow band along the reefs. Sailfish are known to spawn relatively close to land masses rather than in the open ocean (Ueyanagi 1974c) and black marlin are often found nearshore (Nakamura 1985); blue marlin are truly oceanic fishes (Nakamura 1985; Nishikawa et al. 1985). Yet larvae of all three were concentrated in a narrow band only 0.25 nmi (possibly to 1 nmi) off the reef crest. If pelagic fishes such as istiophorids concentrate their spawning very close to reefs or if the larvae are retained there, it will be essential for such areas to be included in studies of the larval biology of these fishes. The assumption that open oceanic areas are the important nursery areas for epipelagic fishes seems at best questionable for istiophorids in the Coral Sea and similar factors may apply to other taxa in this and other areas. For example, Miller (1979) reported much higher concentrations of yellowfin tuna larvae, *Thunnus albacares*, in areas 200 m off the Oahu shoreline than had been reported elsewhere.

Nearshore or near-reef areas may provide more favourable habitats for fish larvae, including those of many pelagic species, than do oceanic areas. The larvae of jack mackerel, *Trachurus symmetricus*, an epipelagic (albeit, neritic) fish, are spread widely over oceanic and coastal areas off California, yet larval mortality due to starvation in oceanic areas can be much higher than in coastal areas, presumably because of insufficient concentrations of food offshore (Theilacker 1986). This may apply to other pelagic fishes as well and

is a further indication that very nearshore (and near-reef) areas must not be excluded from studies of the larvae of epipelagic fishes.

In summary, we found the highest concentrations and abundances of istiophorid larvae of three taxa very close to the windward face of the Great Barrier Reef in the Coral Sea in late spring and summer. Size-frequency analysis suggested that these high concentrations of larvae were due to spawning or at least hatching of eggs very close to the reef. The larvae might be retained in this forereef area of supposed downwelling because, at least during the day, they concentrate in the upper few meters of the water column as preflexion larvae and in the neuston as postflexion larvae. These results have potentially important implications for the study of the larval biology of epipelagic fishes.

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PREVALENCE AND EFFECTS OF INFECTION OF THE DORSAL AORTA IN YELLOWFIN TUNA, *THUNNUS ALBACARES*, BY THE LARVAL CESTODE, *DASYRHYNCHUS TALISMANI*

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ABSTRACT

Approximately 60% of small (<3 kg) yellowfin tuna, *Thunnus albacares*, caught near the Hawaiian Islands carry the plerocercoid (larval) stage of the cestode (tapeworm), *Dasyrhynchus talismani*, in their anterior dorsal aortas. Because the worms and the resultant host inflammation appear to occlude the vessel almost totally, we assumed that the parasite could increase natural mortality rates. Tuna could be limited in their ability to capture prey and therefore should show evidence of long- or short-term food deprivation. We measured body weight, fork length, liver weight, heart weight and, in fish captured from one school, RNA/DNA ratios (a measure of short-term growth rate), and otolith weight (a measure of long-term growth rate) from parasitized and unparasitized fish. We found no significant differences between infected and uninfected fish nor any evidence of starvation in infected fish. How small yellowfin tuna remain apparently unaffected by the parasitic occlusion of their dorsal aorta remains to be demonstrated.

We also examined changes in incidence of infection in small yellowfin tuna caught between February 1985 and March 1986 as well as the prevalence in large (>45 kg) fish. Large yellowfin tuna were rarely parasitized (5.2%) in the dorsal aorta, but showed a high rate (>80%) of infection within other major arteries. The prevalence in small fish varied dramatically with season, dropping suddenly from 66% in June-July 1985 to 11% in August-September 1985. Unparasitized fish caught during August-September 1985 showed significantly higher condition factors, relative heart weights, and relative liver weights than did unparasitized fish caught at other times of the year. We hypothesize that the sudden decrease in prevalence was due to influx of a separate group of small yellowfin tuna into the Hawaiian fishery. We believe that this parasite may therefore serve as a marker for tracing the movements of small yellowfin tuna into and out of specific fisheries or areas.

During a series of experiments that involved catheterization of the anterior dorsal aorta of small (1-3 kg) yellowfin tuna, *Thunnus albacares*, we discovered that approximately 60% of the experimental fish had this blood vessel infected with parasites. The parasites were white, round (2-4 mm in diameter), often more than 4 cm long, and usually folded repeatedly. As a result of the parasites and the tissue inflammation that develops as part of host immune response, the lumen of the infected aortas appeared almost totally occluded. Because all the blood to the internal organs and swimming muscles must flow past this occlusion, we assumed the parasite could be a major factor contributing to the natural mortality of small yellowfin tuna.

The first demonstration of a dorsal aorta parasite in yellowfin tuna was by Kishinouye (1923), who stated, "Often a species of nematod [sic] is found in the dorsal aorta of *Neothunnus macropterus* [now *Thunnus albacares*]; the parasite causes the tissues of the canal to become thick and tough, giving it at the same time a yellowish tint." Other investigators described intravascular parasites from the branchial vessels and arteries serving the stomach, liver, spleen, pyloric caecum, and gall bladder of this species (Baudin Laurencin 1971). The parasites have been described simply as the plerocercoids (larval cestodes) (Chen and Yang 1973), identified to the family Dasyrhynchidae (Ward 1962), or as the species *Dasyrhynchus talismani* (Baudin Laurencin 1971).

Intravascular infection by plerocercoids has been reported from yellowfin tuna caught in the western Pacific (Chen and Yang 1973), eastern Atlantic (Baudin Laurencin 1971), Gulf of Mexico (Ward 1962), and now central Pacific (this report). Infection rates have been reported to be as high as 100% (Baudin Laurencin 1971). If all re-

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ports involve the single parasite species, *D. talismani*, this parasite is both common and ubiquitous.

Because of the apparent vessel blockage by parasites and tissue inflammation, we hypothesized that infected fish would be severely activity limited and not function well as predators. If so, infected fish should show evidence of short- and/or long-term food deprivation, including lower relative condition factors, smaller livers, and slower long- and short-term growth rates (Bulow 1970; Pollard 1971, 1973; Bulow et al. 1981). We also expected blockage of the dorsal aorta to cause increased blood pressures, increased cardiac work, and therefore cardiac hypertrophy (Poupa and Ostadal 1969).

To test our hypotheses, we measured fork length, body weight, liver weight, and ventricle weight from parasitized and unparasitized fish. We also determined RNA/DNA ratios as a measure of the parasite's effects on short-term growth rates (Bulow 1970; Bulow et al. 1981), and relative otolith weights as a measure of the parasite's effects on long-term growth rates. Since otolith weights are linearly related to a fish's chronological age (Boehlert 1985), fish that are older at a given body size should have relatively heavier otoliths. We also recorded the prevalence of infection in small (<3 kg) and large (>45 kg) yellowfin tuna, and in skipjack tuna, *Katsuwonus pelamis*, kawakawa, *Euthynnus affinis*, and bigeye tuna, *T. obesus*. Additionally, monthly prevalence in small yellowfin tuna was noted.

To measure directly the effect of the occlusion caused by the parasites and host inflammation, we used an in vitro perfusion test. We measured the pressure required to push various saline flow rates down the dorsal aorta in freshly dead infected and uninfected fish.

MATERIALS AND METHODS

Sampling Procedures

The small tunas (0.2-3 kg body weight) used in this study were captured at sea near Oahu, HI, returned alive to be held in shoreside tanks at the Kewalo Research Facility (National Marine Fisheries Service, Southwest Fisheries Center Honolulu Laboratory), or sacrificed at sea and held on ice. During necropsy, fork length and body weight were measured, ventricles and livers were removed, blotted dry, and weighed to the nearest 10 mg. Only those fish in captivity for 3 days or less were included in the data for condition factor, and relative heart and liver weights. Large yellowfin tuna (>45 kg body weight) were examined at the Honolulu Fish Auction for the presence of dorsal aorta parasites while the fish were being prepared for sale. All fish were examined within 24 hours of death.

Thirty-five live yellowfin tuna, from one school, were caught 15 January 1986 and transported alive to the Kewalo Research Facility. Immediately upon arrival, the animals were sacrificed, weighed, and measured. Lateral white muscle samples were taken within 4 minutes of death and immediately frozen on dry ice. These samples were subsequently used for measurement of RNA/DNA ratios using the Schmidt-Thannhauser procedure as described in Murno and Fleck (1966). The ventricles and livers of the fish were also removed, blotted dry, and weighed to the nearest 10 mg. Sagittal otoliths were removed, cleaned, dried, and weighed to the nearest microgram.

Parasites for species identification were obtained most often from the major artery within the spleen of large (>45 kg) yellowfin tuna. After being removed from a surrounding capsule, parasites were placed in tap water until the holdfasts everted.

For histological examination, sections of dorsal aorta were fixed in 10% buffered formalin and processed by routine laboratory procedures. Tissue sections were stained with hematoxylin and eosin.

Direct Measurement of Pressure-Flow Relationships in the Anterior Dorsal Aorta

To quantify blockage, we choose to measure the pressures required to push various flow rates of saline through the anterior dorsal aorta of infected and uninfected fish. The dorsal aorta of freshly killed fish was exposed from the confluence of the efferent arteries of the first and second gill arches to the point where it enters the first hemal arch. All efferent and afferent vessels were tied off except for the confluence of the efferent arteries from either the left or right first and second gill arches. This portion of the vessel was cut and a short length of flared polyethylene tubing (PE160, 2.4 mm OD) inserted. The dorsal aorta was also transected at the point where it entered the first hemal arch to allow the saline perfusate to flow out. Parasites were never found poste-

rior to this point. Saline perfusion pressures, at various constant flow rates provided by an infusion pump, were recorded via a Uonix[4] pressure transducer.

Calculation of Relative Condition Factor and Relative Organ Weights

Use of relative condition factor, and relative organ and otolith weights allow groups of fish containing individuals of a range of body sizes to be directly compared (Pollard 1972). Using data from unparasitized fish, regressions of body weight (g) on fork length (cm), liver weight (g) on body weight (g), and heart weight (g) on body weight, were fitted by a least squares technique to the exponential equation:

$$Y = a \cdot X^b$$

using a log-log transformation of the data. Relative condition factor and relative organ weights for individual fish were calculated using the regression parameters (a, b) with the equation:

$$K = W/a \cdot X^b.$$

For relative condition factor, W = body weight and X = fork length. For relative organ weights, W = liver or heart weight, and X = body weight.

The relationship of otolith weight (mg) to body weight was found best fit with the simple linear regression:

$$Y = a + (b \cdot X).$$

Relative otolith weights were therefore calculated using the equation:

$$K = W/(a + b \cdot X)$$

where W = otolith weight and X = body weight.

A relative condition factor <1 indicates that an individual is lighter for its fork length than predicted based on data from unparasitized fish. Similarly, a relative liver or heart weight <1 indicates a smaller liver or heart for a given body size than that found for unparasitized fish. A relative otolith weight >1 means that an individual experienced a relatively slower long-term growth rate (i.e., is relatively older for a given body size and therefore has a larger otolith).

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

Identification of the Parasite

Tapeworms (class: Cestoda, order: Trypanorhyncha) can be identified to species based on scolex morphology and tentacular hooks (onchotaxy), mature segments are not required. The larval cestodes recovered from the yellowfin tuna during this study showed proboscis chainettes flanked by a single row of intercalary hooks, a characteristic that distinguishes *Dasyrhynchus talismani* from its congeners.

This parasite was originally described from five mature worms removed from the spiral valve of *Galeus glaucus* (= *Prionace glauca*, the blue shark) off Cape Verde, West Africa (Dollfus 1935). *Dasyrhynchus talismani* has also been reported in the Pacific from *Carcharinus longimanus* (Heinz and Dailey 1974). All other reports describe plerocercoids from the vascular systems of teleost fishes (Bussieras and Aldrin 1965; Baudin Laurencin 1971; Chen and Yang 1973).

Prevalence of Infection by Host Species, Fish Size, and Season

A total of 53 skipjack tuna, 27 kawakawa, 10 bigeye tuna, and 470 yellowfin tuna were examined for the presence of parasites. We found only yellowfin tuna to be infected.

Infection in yellowfin tuna varied with size class. We found a significantly lower incidence of dorsal aorta infection in large fish. Of 220 individuals weighing 0.21 to 2.7 kg, 48% were infected, while of 250 fish weighing more than 45 kg, only 5.2% carried the parasite in their dorsal aortas. Viscera of a small subsample (N = 8) of the larger fish were examined and indicated that in larger fish the parasite infects (in the order of prevalence) the major arteries of the spleen, intestinal caeca, liver, mesenteries, and lateral blood vessels. Fish in intermediate size classes were not available for this study. Fish >3 kg do not survive the trip from the fishing grounds to the Kewalo Research Facility and are therefore not normally captured by commercial fishermen for return to the laboratory. Fish <45 kg are not common at the Honolulu Fish Auction where they could be examined during normal processing. The

purchase of intermediate-sized yellowfin tuna specifically for this study (yellowfin tuna intended for market cannot be necropsied and then sold) was prohibitively expensive.

Infection of yellowfin tuna appears to vary seasonally. Figure 1 shows changes in prevalence of dorsal aorta infection in small (<3 kg) yellowfin tuna captured between February 1985 through March 1986. Prevalence remained stable for approximately 6 months during the winter through early summer. Then in late summer of 1985, prevalence dropped dramatically from 66 to 11%. Beginning in October 1985, prevalence increased steadily, reaching 39% in February-March 1986, the last months for which data are available.

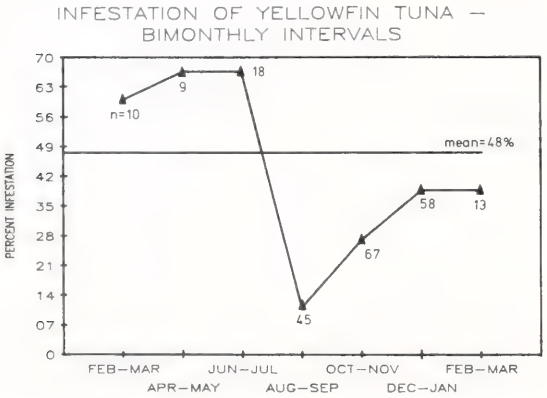

FIGURE 1.—Prevalence (percent infection) of the dorsal aorta by the plerocercoid stage of the cestode *Dasyrhynchus talismani* in small (0.3-3 kg) yellowfin tuna caught near the Hawaiian Islands from February 1985 to March 1986.

Pathology

In infected fish, the anterior dorsal aorta was partially to nearly completely occluded by a parasitic embolus which contained one to several larval cestodes. Figure 2a shows this vessel in a moderately infected yellowfin tuna. Parasites and a small amount of host inflammation are evident in the anterior end (to the right). A normal portion of vessel, with a smooth wall, is seen to the left. Figure 2b shows the anterior dorsal aorta from a very heavily infected fish.

Histological examination revealed that parasitic emboli were primarily composed of larval cestodes, mononuclear cells with eosinophilic granules (presumed to be eosinophils), epitheloid cells (histocytes), fibroblasts, and collagen fibers (Fig. 3). Larval cestodes within the dorsal aorta were associated with a chronic severe endarteritis and, to a lesser extent, mesoarteritis. In heavily infected fish, collapsed channels were commonly found within emboli. Undoubtedly these channels expanded in life with increases in intraluminal blood pressure to allow blood to flow through the vessel. Necrotic worms were also seen, suggesting that the host's defense system was at least partially capable of killing the larvae located in the dorsal aorta.

Infection of other arteries was usually by one, or at most two, larger parasites which were never seen to be folded. These parasites had a bulbous anterior end which always pointed downstream. No evidence of host immune response was observed when the parasites were in vessels other than the dorsal aorta.

Effect of Infection on Measures of Physiological Fitness

Mean (±1 SD) relative condition factor and mean (±1 SD) relative organ weight data are given in Table 1 for the fish sampled between May 1985 and September 1986. Table 2 lists the same parameters plus mean relative otolith weight, and mean RNA/DNA ratio for fish sampled from the single school captured on 15 January 1986. Means were compared with Student's two-tailed T test, with $P = 0.05$ taken as the minimum level for statistical significance.

Examination of data from all the fish caught May 1985-September 1986 reveals statistically significant differences in relative liver and heart weights for parasitized and unparasitized fish. On the average, parasitized fish, have 15% smaller livers, and 9% *smaller* hearts than unparasitized fish. Relative condition factors were not significantly different. When data from fish coming from the single school are examined, there are no statistically significant differences in these three parameters, relative otolith weight, or in RNA/

TABLE 1.—Relative condition factor, relative liver weight, and relative heart weight, of yellowfin tuna sampled between May 1985 and September 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
Uninfected	1.00 (±0.10) $N = 109$	1.02 (±0.22) $N = 82$	1.01 (±0.18) $N = 88$
Infected	0.976 (±0.057) $N = 35$	0.867 (±0.098)* $N = 22$	0.919 (±0.085)* $N = 32$

*Uninfected and infected groups different at $P = 0.05$ level.

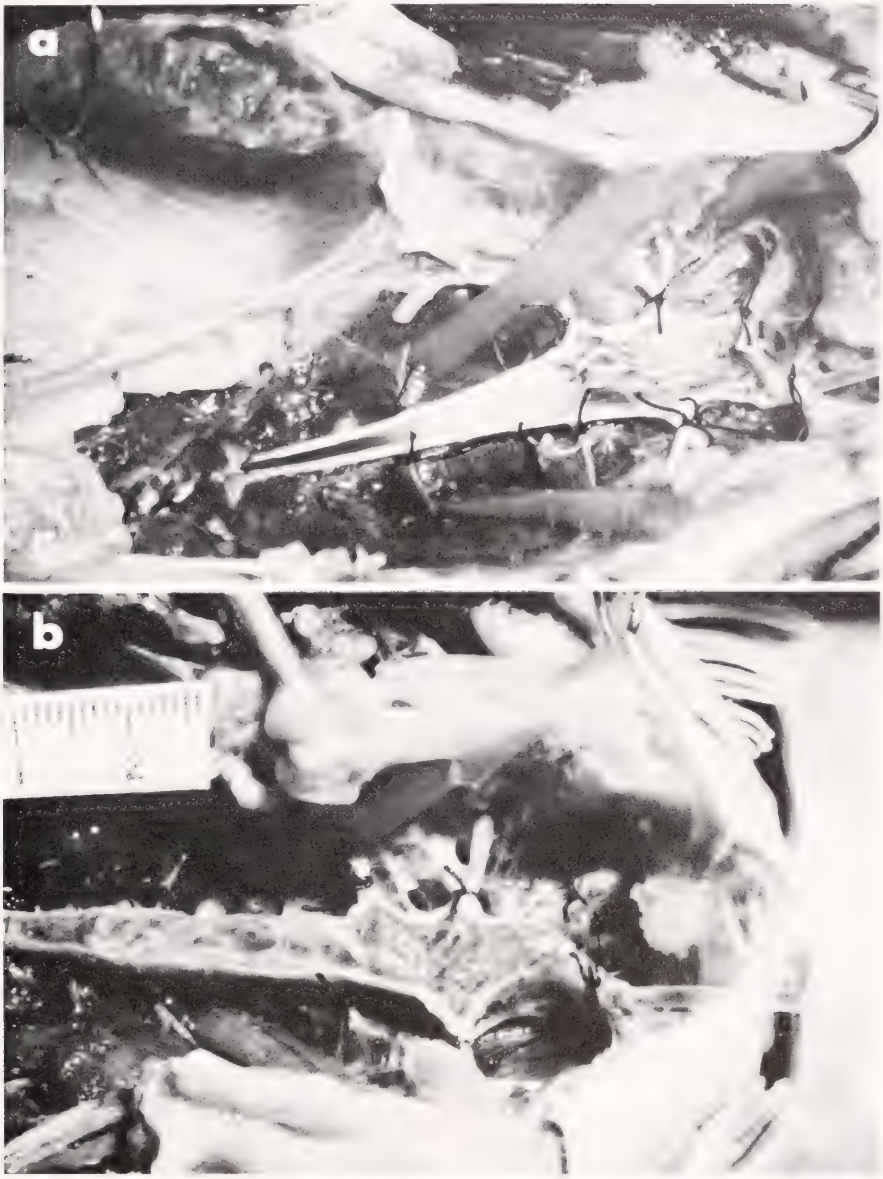

FIGURE 2a.—The anterior dorsal aorta of a moderately infected yellowfin tuna. In the anterior end of the vessel (to the right) are parasites and host inflammation.

FIGURE 2b.—The anterior dorsal aorta of a heavily infected yellowfin tuna. The vessel's lumen is all but occluded by parasites and host inflammation. Ruler divisions are in mm.

TABLE 2.—Relative condition factor, relative liver weight, relative heart weight, relative otolith weight, and RNA/DNA ratio of yellowfin tuna sampled 15 January 1986.

Fish	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight	Mean (±SD) relative otolith weight	Mean (±SD) RNA/DNA ratios
Uninfected	1.00 (±0.04) $N = 23$	1.00 (±0.08) $N = 23$	1.00 (±0.06) $N = 23$	1.00 (±0.04) $N = 12$	28.9 (±8.9) $N = 21$
Infected	0.995 (±0.035) $N = 12$	1.00 (±0.07) $N = 12$	0.975 (±0.074) $N = 12$	0.980 (±0.058) $N = 8$	33.1 (±11.1) $N = 10$

FIGURE 3.—Photomicrograph of a cross section of the dorsal aorta containing parasites and host inflammation of a heavily infected yellowfin tuna. The host inflammation (I) and cross sections of the parasites (W) can be easily differentiated. Hematoxylin and eosin stain.

DNA ratios. RNA/DNA ratios were compared directly (rather than by calculating relative RNA/DNA ratios) because they were found not to be correlated with body weight (correlation coefficient = 0.04).

Data from *unparasitized* fish collected in August and September 1985 were analyzed separately from all remaining *unparasitized* fish. This was done because we found dramatically lower rates of infection (11%) during those 2 months than during the preceding 2 months (67% infected) and assumed this to be due to an influx of a new group of small yellowfin tuna into the Hawaiian fishery. New regression parameters for body weight on fork length, heart weight on body weight, and liver weight on body weight were calculated using data from unparasitized fish excluding those caught during August-September 1985. Mean relative condition factors and relative organ weights were then recalculated.

Table 3 shows mean relative condition factors, mean relative liver weights, and mean relative heart weights for unparasitized fish captured during August and September 1985, unparasitized

TABLE 3.—Relative condition factor, relative liver weight, and relative heart weight from uninfected yellowfin tuna sampled during August and September 1985, from all other uninfected yellowfin tuna, and all infected fish.

Group	Mean (±SD) relative condition factor	Mean (±SD) relative liver weight	Mean (±SD) relative heart weight
August-September 1985 uninfected fish	1.11 (±0.08)* $N = 36$	1.24 (±0.28)* $N = 35$	1.22 (±0.18)* $N = 36$
All other uninfected fish	1.00 (±0.09) $N = 73$	1.01 (±0.17) $N = 47$	1.00 (±0.09) $N = 52$
Infected fish	1.01 (±0.06) $N = 35$	0.937 (±0.102) $N = 22$	1.00 (±0.09) $N = 32$

*Uninfected groups different at $P = 0.01$ level.

fish captured at all other times of the year, and all parasitized fish, based on the new regression parameters. The two groups of *unparasitized* fish show statistically significant differences in all three. Fish caught during August and September were on the average 11% heavier at a given body size (i.e., relative condition factor = 1.11), had livers an average of 23% heavier, and had hearts an average of 22% heavier than those unparasitized fish captured at other times of the year. When unparasitized fish, excluding those caught during August and September, are compared with parasitized fish, there are now no statistically significant differences in mean relative condition factors, mean relative liver weights, or mean relative heart weights. The data from unparasitized fish captured in August and September, when included in the complete data set, are therefore responsible for the observed differences in relative heart and liver weights between infected and uninfected fish seen in Table 1.

In Vitro Perfusion of the Dorsal Aorta

Three parasitized and five unparasitized fish, ranging in weight from 0.915 to 2.666 kg, were used in this series of experiments. The intensity of infection was subjectively classified as slight, moderate, or heavy. Perfusion pressures were normalized to a 1 kg fish weight by dividing the observed pressures by the reciprocal of body weight, in kilograms. Moderately and heavily infected fish showed higher perfusion pressures at a given flow rate than did unparasitized animals (Fig. 4). While no data are available on the normal cardiac outputs and blood pressures in swimming yellowfin tuna, restrained and lightly anesthetized yellowfin tuna have cardiac outputs of approximately 40-60 mL/kg and dorsal aorta blood pressures of 50-70 mm Hg (D. R. Jones and R. W. Brill, unpubl. obs.). Figure 4 shows that at normal cardiac outputs, the apparent occlusion of the dorsal aorta caused by the parasites and host inflammation is indeed real and should cause moderately and heavily infected fish to have excessively high blood pressures, high cardiac energy demands and presumably reduced fitness.

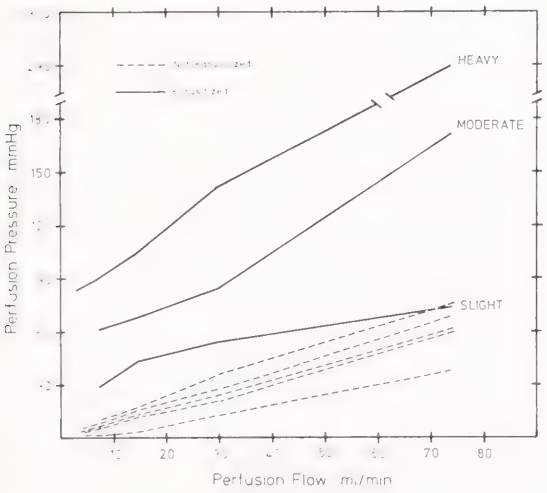

FIGURE 4.—In vitro pressure required to pump various rates of saline down the dorsal aorta of parasitized and unparasitized yellowfin tuna. The fish ranged in size from 0.915 to 2.666 kg. Data have been normalized to a body weight of 1 kg.

DISCUSSION

Prevalence of Infection by Species, Size, and Season

Our data indicate that in Hawaiian waters *D. talismani* is limited to yellowfin tuna. However, *D. talismani* has been reported to occur in Atlantic bigeye tuna (Bussieras and Aldrin 1965). Since we examined relatively few individuals of this species, we cannot rule out the occurrence of this parasite in bigeye tuna in the central Pacific.

Skipjack tuna, bigeye tuna, kawakawa, and yellowfin tuna often occur simultaneously in the same areas and show a great overlap in prey species (King and Ikehara 1956; Waldron and King 1963). It is therefore unlikely that host specificity is attributable to only yellowfin tuna ingesting the intermediate host, which is not known but is most likely a small crustacean (Deardorff et al. 1984). Host specificity could arise if the procercoid of *D. talismani* is not stimulated or is unable to penetrate the gut wall of tuna species other than yellowfin tuna, or that species of tuna other than yellowfin are capable of immune rejection (Orr et al. 1969).

The reasons for the dramatic decrease in incidence of dorsal aorta infection in large (>45 kg) yellowfin tuna are unknown. Possible reasons include procercoids ingested less frequently by larger animals, host destruction of the parasite, increased mortality of parasitized fish, or movement of the parasite out of the dorsal aorta into other major arterial vessels. Of these alternatives, increased mortality of infected fish seems unlikely.

While we did not demonstrate directly the pre-

ence of antibodies against the parasite, several histological cross sections show worms in stages of degeneration, and host destruction of larval and adult cestodes has been shown in other teleosts (Kennedy and Walker 1969; Smith 1973; MacKenzie 1975). Examination of a small number of pyloric caeca, liver, spleen, lateral arteries, and stomach vasculature of large yellowfin tuna (>45 kg) showed >85% infection, suggesting 1) that the parasite may move out of the dorsal aorta into other large arteries as yellowfin tuna grow, 2) that the host response to the parasite may be less vigorous in vessels other than the dorsal aorta, and/or 3) that the parasite may preferentially select other vessels in larger fish. Baudin Laurencin (1971) found a decrease in branchial artery infection of yellowfin tuna with increasing body size, but no change in rates of infection of abdominal vessels.

The change in the rate of infection seen in August and September 1985 in small yellowfin tuna (Fig. 1) is, we believe, due to a large influx of uninfected fish into the Hawaiian fishery. Although we have no direct corroborating evidence, such as increased catch per unit effort for this size yellowfin tuna at that time, Tester and Nakamura (1957) have shown that there are repeated influxes of small yellowfin tuna into areas near the main Hawaiian Islands during late summer and early fall. Furthermore, the dramatic differences seen in relative condition factors, relative liver weights, and relative heart weights between unparasitized fish caught during August-September 1985, and the remaining unparasitized fish, clearly imply that the former group had a different history.

We have no evidence nor are we hypothesizing that these groups come from genetically isolated subpopulations. We do believe, however, that the two groups were separate most likely since hatching. We do not know the maximum lifespan of the dorsal aorta parasite, but one yellowfin tuna killed after 172 days in captivity at the Kewalo Research Facility was parasitized. Since fish in captivity are fed only frozen food and their tanks are supplied with filtered seawater (Queenth and Brill[5]), it is unlikely this fish became infected after capture. Yellowfin tuna of the 1-3 kg size range are about 270-360 days old (Uchiyama and Struhsaker 1981) and therefore could have carried the parasite most of their lives.

The slow increase in prevalence from October 1985 through March 1986 remains to be explained, but could be due to emigration of the new group of yellowfin tuna out of the Hawaiian fishery or slowly increasing infection of the new group. This latter explanation implies higher prevalence of the parasite around islands which could be due either to a greater number of final (shark) or intermediate hosts around islands.

Pathology

The severe enarteritis associated with *D. talismani* infection suggests that the parasite is recognized by the fish's defense system as foreign material in the dorsal aorta. Dead worms within the inflammatory tissue imply that the parasite is not well adapted for survival in this location. Presumably, *D. talismani* would elicit, and be attacked by, a similar inflammatory response irrespective of its location within the vasculature. This response was not observed in other vessels and additional work is needed to clarify the site specificity of the immune response. Our findings also suggest that cellular elements are responsible for the destruction of the larval cestodes when located in the dorsal aorta.

Effect of the Infection of the Dorsal Aorta on Natural Mortality

We found no evidence to support our original hypothesis that infected yellowfin tuna are activity limited and therefore less able to secure food. When the data from the unparasitized fish caught August-September 1985 are excluded, there are no differences in relative condition factors, relative liver weights, or relative heart weights between parasitized and unparasitized fish. When parasitized and unparasitized fish from the single school caught 15 January 1985 are compared, no significant differences in these parameters, mean short-term (i.e., RNA/DNA ratios), or mean long-term (i.e., relative otolith weights) growth are evident.

Because parasite emboli appear to cause almost complete occlusion of the anterior dorsal aorta (the only blood vessel supplying the viscera and swimming muscles), the lack of differences between infected and uninfected fish was not expected. Overstreet (1977), investigating the effects of plerocercoid infection on sciaenid fishes in

[5]Queenth, M. K. K., and R. W. Brill. 1983. Operations and procedures manual for visiting scientists at the Kewalo Research Facility. Southwest Fish. Cent. Admin. Rep. H-83-7, 16 p. Natl. Mar. Fish. Serv., NOAA, Honolulu, HI.

the Gulf of Mexico, found no apparent detrimental effect on the host, but these parasites were found encysted in the muscle, not the vasculature. Although the ability of parasitized yellowfin tuna to function as predators are apparently not affected, their ability to escape predation remains to be tested. It is possible that infected yellowfin tuna are subjected to differential predation, as has been shown to be for roach, *Rutilus rutilus*, infected in the coelomic cavity by the plerocercoid of *Ligula* sp. (Van Dobben 1952).

Pressure Flow Relationships in the Dorsal Aorta

The unphysiologically high pressures required to pump saline through the dorsal aortas of moderately and heavily infected fish remain to be explained in light of apparent lack of effects of the parasite on other measures of the fish's condition, including the absence of cardiac hypertrophy. It is possible that the dorsal aorta, because of its thick muscular wall (J. Brock, unpubl. obs.), becomes significantly less compliant postmortem. Such changes could require that higher pressures be generated to create a given degree of expansion. Therefore higher pressures would be required postmortum to push a given flow rate of saline through the vessel.

In summary, *D. talismani* appears to have no significant adverse effects on the physiological fitness and natural mortality of small yellowfin tuna in spite of apparent vascular blockage. How these fish are able to cope with dorsal aorta infection requires further investigation.

Use of *Dasyrhynchus talismani* as a Natural Tag for Tracing Movements of Small Yellowfin Tuna

We feel that this parasite offers excellent potential as a natural marker for tracking the movements of separate groups of small yellowfin tuna between or into specific fisheries. (For a review of the use of parasites to delineate stocks for management purposes, see MacKenzie 1983.) *Dasyrhynchus talismani* does not fulfill all seven requirements for an ideal natural tag listed by Sindermann (1983), but it does appear to meet the requirements of 1) having significant differences of geographic prevalence, 2) being easily detected, 3) being able to be definitively identified, 4) having minimum effect on host survival, and 5) surviving in the host for long periods. Data on prevalence of *D. talismani* could be combined with data on prevalence of other parasites, as has been shown by Lester et al. (1985) for skipjack tuna, or combined with data on relative condition factor, relative heart weight, and relative liver weight to provide information on fish movements.

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AGE AND GROWTH OF SPANISH MACKEREL, *SCOMBEROMORUS MACULATUS*, FROM FLORIDA AND THE GULF OF MEXICO

WILLIAM A. FABLE, JR., ALLYN G. JOHNSON, AND LYMAN E. BARGER[1]

ABSTRACT

Otoliths from 1,787 Spanish mackerel, *Scomberomorus maculatus*, were used to estimate age and growth rates of this species from Florida and the Gulf of Mexico. There was a wide range of lengths within an age group: the oldest male was 7 years old, while the oldest female was 9 years old. Length at age was significantly different for sexes, sampling areas, and collection gear. The von Bertalanffy growth equations were as follows: males (all areas combined) $l_t = 794\ (1 - e^{-0.24(t + 0.94)})$; females (all areas combined) $l_t = 739\ (1 - e^{-0.33(t + 0.99)})$; males (Florida only) $l_t = 776\ (1 - e^{-0.27(t + 0.73)})$; females (Florida only) $l_t = 731\ (1 - e^{-0.38(t + 0.73)})$, where l = fork length (mm) and t = years.

Spanish mackerel, *Scomberomorus maculatus*, are found in the western Atlantic Ocean from the Gulf of Maine to the Yucatan Peninsula (Collette et al. 1978), and have their center of abundance off Florida (Trent and Anthony 1978). They support extensive commercial and recreational fisheries in the U.S. south Atlantic and Gulf of Mexico. In 1985, U.S. commercial landings totaled 5.8 million pounds (2,631 t) (U.S. Department of Commerce 1986a) while recreational landings were estimated to be 2.1 million pounds (953 t) (U.S. Department of Commerce 1986b). Information on Spanish mackerel published prior to 1978 actually concerned two species, *S. maculatus* and *S. brasiliensis* (Collette et al. 1978). Collette et al. (1978) determined that Spanish mackerel south of the Yucatan Peninsula (on the Central and South American Atlantic coasts) are *S. brasiliensis*, and those along U.S. coasts are *S. maculatus*.

There is disagreement in the literature on the interpretation of annuli on otoliths of Spanish mackerel. The first information on age and growth of *S. maculatus* was from fish collected in southeast Florida (Klima 1959). Later, Mendoza (1968) gave some limited age and growth information on *S. maculatus* from Veracruz, Mexico, and Powell (1975) provided the most recent information on Spanish mackerel age, growth, and reproduction in Florida. Powell interpreted annuli on Spanish mackerel otoliths differently than did Klima, and the different age determinations yielded different growth estimates. Mendoza (1968) did not estimate growth except by presenting his data in tabular form.

We undertook this investigation to resolve these uncertainties in the literature and to derive more current age and growth parameters. This information will provide a better basis for rational management of this species.

STUDY AREA AND METHODS

We collected 1,929 Spanish mackerel from 1977 through 1981 from the south Atlantic and Gulf of Mexico coasts of the United States. Most (1,422) of the fish came from northwest Florida and only 10 came from north of south Florida on the Atlantic coast (Table 1). Fork length (FL) of each

TABLE 1.—Numbers of Spanish mackerel collected for age and growth study.

Area	Year					Total
	1977	1978	1979	1980	1981	
Texas	—	48	—	—	—	48
Mississippi/ Louisiana	41	79	—	23	—	143
Northwest Florida	59	377	31	955	—	1,422
South Florida	—	87	31	59	129	306
Georgia	—	10	—	—	—	10
Total	100	601	62	1,037	129	1,929

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mackerel was measured to the nearest millimeter. Sagittal otoliths were removed, washed, and stored dry. The clearest, most legible otolith from each fish (based on visual observation) was examined to estimate age and growth.

Whole otoliths were placed in a black-bottomed watch glass containing 100% glycerin and examined with a binocular microscope at 28× using reflected light. Otolith radius (OR) was measured in ocular micrometer units (1 unit = 0.0363 mm) on the posterior surface from the focus to the distal margin along the axis of the sulcus acousticus (Powell 1975). Growth marks were counted and measured from the focus along the radius to their distal edge. The marks were opaque (light) under reflected light, while the interspaces were hyaline or translucent (dark).

Otoliths were classified into age groups based on the number of opaque nonmarginal marks (Powell 1975). A mark was considered complete when a hyaline (dark) interspace or margin was visible from successive growth. Three readers independently examined each of 520 otoliths to test the precision of our ageing technique. This information was analyzed using the method of Beamish and Fournier (1981). All other otoliths were independently examined by two readers; if their results did not agree, the data were not used.

To compare age estimates based on surface (whole) and internal (sectional) examination, we sectioned 70 otoliths which had been previously examined on the surface (2-10 otoliths from different fish from each age 0+ through 8+), following the methods of Johnson et al. (1983).

We determined time of annulus formation and validated our ageing technique by comparing monthly percentage frequencies of otoliths with opaque margins. A high percentage frequency (>45%) indicated recent annulus formation. We used a chi-square test to compare the monthly frequencies.

The relationship between otolith radius and fork length was determined and used to back calculate fork lengths at earlier ages (Tesch 1971; Ricker 1975; Everhart et al. 1975). We used analysis of covariance (ANCOVA) with age as the covariate to test for differences in growth rates (lengths at age) of fish collected in different locations, by different gears, and of different sexes. Mean back-calculated lengths were used to calculate von Bertalanffy (1938) growth parameters, employing a computer program developed by Abramson (1971).

RESULTS AND DISCUSSION

Validation

Age validation has often been overlooked in the age and growth literature (Beamish and McFarlane 1983). Although there are numerous methods available to establish the annual nature of otolith growth rings, we applied marginal increment analysis, because it was the only practical method to use on this migratory, pelagic species.

Annulus formation occurred in March, April, or May (Fig. 1). A chi-square test ($\chi^2 = 338.47$, $df = 1, P < 0.001$) showed a highly significant difference between the occurrence of otoliths with opaque margins in these months versus the other nine months of the year. Our findings are in agreement with Powell (1975) in that the main period of opaque mark formation was in the spring or early summer. He reported mark formation in May, June, and July by examination of marginal increments. Previously Klima (1959) described both summer and winter growth rings and evaluated the marginal condition to decide that marks were deposited annually. Our observations on the appearance of annuli in Spanish mackerel otoliths agreed with Powell (1975), in that we also were unable to discern the "first winter mark" that Klima (1959) described.

Age

To estimate the precision of our ageing, we compared sections to whole otoliths and evaluations by different readers. Examination of 70 sectioned otoliths provided a 97.4% agreement with previous surface examination of the same otoliths. Surface age determinations of three readers on 520 otoliths had a 97.7% agreement. Using the technique of Beamish and Fournier (1981), the index of average percent error was 0.3273, which we think is excellent.

Of 1,929 Spanish mackerel examined, 1,787 (92.6%), ranging from 148 to 802 mm FL, were aged. The oldest female was 9 years old, while the oldest male was 7 years old. Powell's (1975) oldest fish, a female, was 8 years old, while Klima's (1959) oldest males and females were both 6 years old. These data and the data presented in Tables 2 and 3 indicate that females live longer than males.

We found a wide range of lengths within an age group for both sexes (Tables 2, 3), as did Powell, with some Spanish mackerel of age 0 through 5 in

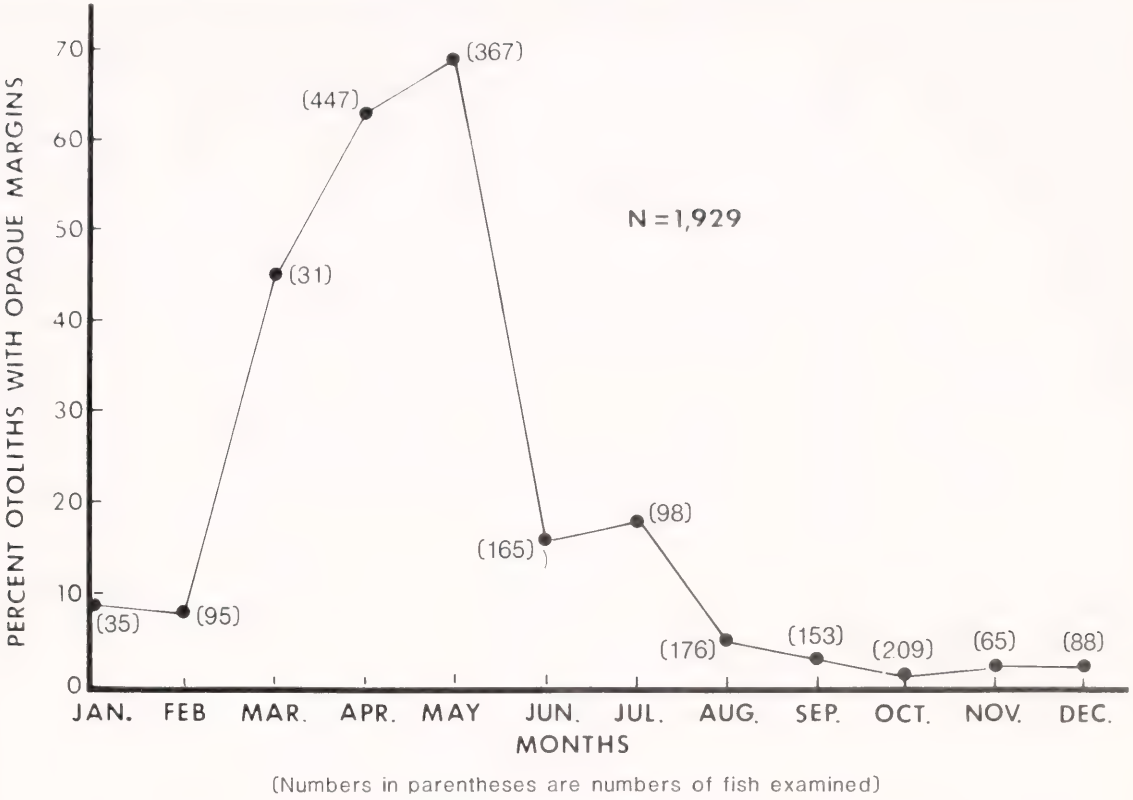

FIGURE 1.—Monthly percentage frequencies of Spanish mackerel otoliths with opaque margins.

the same size interval. In the closely related king mackerel, *S. cavalla*, Johnson et al. (1983) reported a similar situation. Our results substantiate wide variation in growth rates of individual Spanish mackerel.

Growth

Otolith radius (OR) was closely correlated with fish length (FL). The curvilinear relation $FL = 1.5091\ OR^{1.2639}$ ($r = 0.944$) had a slightly better fit than the linear equation $FL = -102.8061 + 6.1295\ OR$ ($r = 0.936$). We used the former equation to back calculate lengths at former ages for 949 fish that had at least one annulus (838 fish had no annuli and were classified as age 0). Neither Klima nor Powell reported any equations for an OR versus FL relationship.

The mean back-calculated annual increments of fork lengths for male and female Spanish mackerel from all areas and years combined (Tables 4, 5) indicate that growth rates were rapid until age 5 in females and to age 6 in males (the age 6 increment in males was based on one fish). After these ages, growth rates slowed appreciably. Early growth was more rapid in females than males (first annual increment 123.6 as compared to 98.7). However, males maintained a higher growth rate through age 6, except for age 5, when the female annual increment was 55.3 mm versus 47.9 mm in males.

Our back-calculations for Spanish mackerel showed variation in mean fork lengths at age between sexes, areas, and years (Table 6). Females from south Florida grew faster than any other group and males from there grew faster than any other males. For Spanish mackerel from northwest Florida, where the largest number of fish were collected, analysis of covariance (ANCOVA) indicated significant differences in growth (length-at-age) between sexes and collecting gears (Table 7).

ANCOVA was also used to test the significance of growth differences among geographic areas

TABLE 2.—Fork length (mm) composition, in percent, of male Spanish mackerel by age group (locations combined).

Length group	Age in years							Total number of fish
	0	1	2	3	4	5	7	
175-199	100.0							1
200-224	100.0							1
225-249	100.0							5
250-274	100.0							2
275-299	68.3	31.7						41
300-324	76.5	23.5						102
325-349	51.0	47.1	1.9					155
350-374	47.7	47.7	4.5					88
375-399	20.7	59.8	17.1	1.2				82
400-424	5.5	78.2	14.5					55
425-449	22.2	33.3	22.2	22.2				9
450-474	9.1	54.5	18.2		9.1	9.1		11
475-499		50.0			50.0			2
500-524		16.7	33.3	33.3	16.7			6
525-549		40.0	40.0	20.0				5
550-574			50.0			50.0		2
575-599				33.3	66.6			3
600-624								0
625-649						100.0		3
650-674								0
675-699							100.0	1
700-724						100.0		1
Total								575

TABLE 3.—Fork length (mm) composition, in percent, of female Spanish mackerel by age group (locations combined).

Length group	Age in years										Total number of fish
	0	1	2	3	4	5	6	7	8	9	
175-199	100.0										1
200-224	100.0										2
225-249	80.0	20.0									5
250-274	100.0										3
275-299	96.7	3.3									30
300-324	84.8	13.6	1.5								66
325-349	77.0	23.0									152
350-374	52.4	46.4	1.2								166
375-399	46.7	51.1	2.2								137
400-424	41.1	52.5	5.7	0.7							141
425-449	22.8	62.4	12.9	2.0							101
450-474	25.3	49.3	20.0	2.7	1.3		1.3				75
475-499	8.1	48.4	40.3	3.2							62
500-524	5.3	52.6	31.6	8.8		1.8					57
525-549	1.9	39.6	32.1	17.0	9.4						53
550-574		25.0	22.5	37.5	15.0						40
575-599		5.0	30.0	40.0	2.5						40
600-624		5.9	23.5	41.2	23.5	5.9					17
625-649			13.6	45.5	22.7	13.6	4.5				22
650-674			6.3	25.0	25.0	25.0	6.3	6.3	6.3		16
675-699				16.7	33.3	25.0	8.3	16.7			12
700-724						42.9	14.3		42.9		7
725-749				16.7		33.3		16.7	16.7	16.7	6
750-774											0
775-799							100.0				1
Total											1,212

TABLE 4.—Mean back-calculated fork lengths (mm) at age for male Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age							
			1	2	3	4	5	6	7	
I	363.9	237	296.9							
II	413.7	33	306.4	382.2						
III	488.1	7	318.2	415.4	458.2					
IV	536.8	4	353.8	423.5	483.9	529.8				
V	605.0	5	374.9	448.2	522.4	567.1	596.3			
VI	—	0	—	—	—	—	—	—		
VII	679.0	1	342.0	521.8	570.9	606.5	642.5	657.1	671.7	
		287	300.8	399.5	489.8	556.1	604.0	657.1	671.7	Weighted mean
				98.7	90.3	66.3	47.9	53.1	14.3	Annual increment

TABLE 5.—Mean back-calculated fork lengths (mm) at age for female Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age									
			1	2	3	4	5	6	7	8	9	
I	420.1	437	344.6									
II	503.6	113	340.8	463.1								
III	580.9	62	349.2	480.2	550.8							
IV	596.7	30	356.9	471.1	529.2	580.0						
V	682.0	11	359.9	471.0	565.1	625.4	666.6					
VI	683.0	3	405.1	472.9	546.5	602.5	643.7	673.7				
VII	654.7	3	324.1	431.8	485.4	529.2	572.3	617.3	645.7			
VIII	696.0	2	329.7	458.9	521.0	557.6	615.2	649.6	670.5	688.0		
IX	737.0	1	399.0	470.0	529.0	596.7	653.4	685.3	704.6	717.5	730.5	
		662	345.4	469.0	543.8	587.9	643.2	650.8	663.8	697.8	730.5	Weighted mean
				123.6	74.8	44.1	55.3	7.6	13.0	34.0	32.7	Annual increment

TABLE 6.—Weighted means of back-calculated fork lengths (mm) for male and female Spanish mackerel from all areas and years having appreciable numbers (over 100) of mackerels sampled.

Age group	All locations			Northwest Florida			Louisiana	South Florida		All Florida
	1978	1980	1981	1978	1980	All years	All years	1981	All years	All years
Males										
I	285	303	356	281	300	293	321	384	332	299
II	356	403	465	347	392	380	384	483	438	399
III	[1]448	474	531	[1]470	[1]460	[1]463	[1]440	558	508	494
IV		538	584		[1]529	[1]529	[1]479	607	566	561
V		[1]561	652		[1]561	[1]561	[1]454	[1]652	[1]654	[1]631
VI			[1]657					[1]657	[1]657	[1]657
VII			[1]672					[1]672	[1]672	[1]672
Females										
I	325	347	371	326	346	342	334	366	364	348
II	428	465	507	434	466	454	436	509	500	475
III	492	526	573	486	536	517	500	574	573	557
IV	[1]564	518	614	[1]555	[1]542	[1]548	518	615	614	607
V		[1]485	655				[1]536	655	654	654
VI		[1]540	665				[1]540	665	665	665
VII		[1]572	682				[1]572	682	682	682
VIII			[1]698					[1]698	[1]698	[1]693
IX			[1]730					[1]730	[1]730	[1]730

[1]Lengths based on less than 5 fish

TABLE 7.—Results of analysis of covariance for growth differences observed in Spanish mackerel collected in northwest Florida, and fish collected in all areas by recreational hook and line, and gill net.

Source	Sum of squares	df	Mean square	*P*	Tail probability
Gill net					
Gear	2,499.15	2	1,249.57	13.04	0.00
Sex	5,275.31	1	5,275.31	55.03	0.00
Gear × sex	136.80	2	68.40	0.71	0.49
Age	41,384.91	1	41,384.91	431.73	0.00
Error	75,440.13	787	95.86		
n = 794					
NW Florida					
Area	3,792.09	2	1,896.05	22.83	0.00
Sex	476.13	1	476.13	5.73	0.02
Area × sex	689.00	2	344.50	4.15	0.02
Age	42,623.18	1	42,623.18	513.16	0.00
Error	38,955.39	469	83.06		
n = 476					
Recreational hook and line					
Area	1,132.44	2	566.22	5.42	0.00
Sex	2,673.83	1	2,673.83	25.59	0.00
Area × sex	183.17	2	91.58	0.88	0.42
Age	124,338.42	1	124,338.42	1,190.00	0.00
Error	78,886.76	755	104.49		
n = 762					

(sex, area × sex, and age were also included in the covariance model) for recreational hook and line samples and gill net samples. Area differences were highly significant for both gear types, and sex differences were highly significant for gill net-caught fish, but somewhat less so for hook and line samples (Table 7). The area × sex interaction was significant for hook and line, but not gill net samples.

These ANCOVA results demonstrate that females grew significantly faster than males. The significant differences between sampling gears are no doubt due to gear selectivity, i.e., hook and line selecting for larger fish of a given age and gill nets selecting for a specific size fish. Significant differences between sampling areas (consistent for both sampling gears) substantiate faster growth in south Florida (fish were larger at a given age) than in northwest Florida or Louisiana.

We compared back-calculated lengths-at-age of Spanish mackerel (from all areas and from Florida alone) with those of Powell (1975); lengths at ages 1 and 2 for both sexes were shorter, while those for ages 3-5 were increasingly longer (Table 8). There was a greater discrepancy between our data and Powell's for males than for females. Florida males from our study were 38 mm shorter than Powell's at age 1, but by age 5 they were 120 mm longer. Florida females from our study were 25 mm shorter than Powell's at age 1, but by age 5 they were 33 mm longer. Some of this discrepancy can be explained by the fact that Powell used the direct proportion method for his back-calculations, whereas the program by Abramson (1971) employs the regression method. Carlander (1981) pointed out potential problems with this method, but they primarily concern the fact that when using the scales for ageing, not all scales on a fish are the same size. This problem is of lesser importance when ageing is done from otoliths.

TABLE 8.—Mean back-calculated fork lengths (mm) at age by sex for Spanish mackerel from Powell (1975) and this study. Powell's data were transformed from standard length by his formula FL = 1.0728 SL + 2.4267.

Age group	Powell		Fable et al.			
			Florida		All areas	
	Males	Females	Males	Females	Males	Females
I	337	373	299	348	301	345
II	421	481	399	475	400	469
III	459	542	494	557	490	544
IV	489	580	561	607	556	588
V	511	621	631	654	604	643
VI			657	665	657	651
VII			672	682	672	664
VIII				698		698
IX				730		731

Our estimates of the von Bertalanffy growth coefficient (k) are smaller, and our asymptotic

lengths (L_∞) are larger (especially for males) than those derived by Powell (1975) and Nomura (1967) (Table 9). Nomura used Klima's (1959) data to compute growth curves for Florida fish. Our L_∞ estimates are much closer to the maximum observed lengths in our samples (802 mm FL female and 723 mm FL male) than were the estimates from other authors. The differences between our estimates and Powell's (1975) are easily explained because we included the oldest fish in our back-calculations, whereas Powell only included fish up to 5 years old, forcing his growth coefficient (k) to be higher. Therefore, we believe our growth parameters are a more accurate reflection of population growth and more appropriate to use in assessment of the status of the stock.

TABLE 9.—Von Bertalanffy growth parameters for Spanish mackerel.

Author	Males			Females		
	K	L_∞ (FL mm)	t_0 (years)	K	L_∞ (FL mm)	t_0 (years)
Fable et al. all areas combined	0.24	794	−0.94	0.33	739	−0.99
Fable et al. Florida	0.27	776	−0.73	0.38	731	−0.73
Powell (1975)	0.48	555	−1.12	0.45	694	−0.78
Nomura (1967) using Klima's (1959) data	0.40	607	+0.15	0.40	720	+0.28

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FEEDING HABITATS OF SPOT, *LEIOSTOMUS XANTHURUS*, IN POLYHALINE VERSUS MESO-OLIGOHALINE TIDAL CREEKS AND SHOALS[1]

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ABSTRACT

Young-of-year spot, *Leiostomus xanthurus*, were collected by otter trawl within tidal creeks and on adjacent shoals in polyhaline and meso-oligohaline zones of the York River, Virginia. Total densities of spot at Blevins Creek, a polyhaline system, were twice that of the meso-oligohaline Goalders Creek.

Stomach content analysis confirmed previous studies of the generally opportunistic feeding strategy of juvenile spot. However, distinct differences in food utilization were observed between creeks and among creek and shoal stations. In addition, prey utilization differences due to habitat generally paralleled seasonal distribution patterns of dominant macrobenthos reported for the area.

Two major ontogenetic groups were distinguished. Small spot (<30 mm SL) consumed more planktonic food items (calanoid copepods) than the larger size classes, which fed on more benthic prey and displayed greater overlap in diet. Small spot tended to be selective; larger spot were more opportunistic.

Tidal salt marshes and their associated drainages are recognized primary nurseries for spot, *Leiostomus xanthurus*, (Herke 1971; Parker 1971; Weinstein 1979; Currin et al. 1984). Shortly after recruitment, young spot tend to concentrate in tidal creeks, and by late spring densities in these creeks are often several times higher than in nearby seagrass habitats or shoal areas (Weinstein and Brooks 1983; Smith et al. 1984). Once recruited to tidal creeks, spot seem to take up residence, with limited movement out of (or between) marshes until the fall mass exodus (Weinstein 1983; Weinstein and Brooks 1983; Currin et al. 1984; Weinstein et al. 1984; Weinstein and O'Neil 1986).

The role of marsh nurseries as predation refuges versus feeding areas is currently under debate (Boesch and Turner 1984). As suggested by the studies of Vince et al. (1976), it is likely that the marsh serves in both capacities. Qualitative and quantitative data on food availability and quality and on differences among habitats will be necessary to resolve the food versus refuge question. Ultimately, these data should be supported by experimental studies on growth rates versus the quality of food resources in different habitats (Weisberg and Lotrich 1982). We report here on one of the steps in the process, a descriptive comparison of gut contents of spot collected in tidal creeks and shoal areas in marshes of two salinity regimes, meso-oligohaline and polyhaline.

Although the food habits of spot have been previously studied, most investigators captured spot in openwater habitats, not in the primary nurseries (Parker 1971; Stickney et al. 1975; Chao and Musick 1977; Sheridan 1979). Only Hodson et al. (1981) studied food utilization of spot in tidal creeks. Their population, however, was restricted mainly to small fish (<40 mm) capable of exploiting the small creek rivulets and susceptible to capture by block net. This study expands the effort of Hodson et al. (1981), and includes the entire seasonal residency period for spot in tidal creeks of the York River estuary, VA. A survey of food utilization was conducted in 1983 for all young-of-year size classes occupying two tidal creeks and nearby river shoals at widely separated salinities. Specific objectives of this effort were to 1) describe food utilization of juvenile spot in each habitat, 2) document any sequential ontogenetic changes in food utilization, and 3) compare the overall food utilization of spot residing in tidal creeks or adjacent shoals dissimilar in salinity. It was anticipated that feeding differences would reflect the availability and types of food in

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the two salinity regimes and microhabitats constituting the creek and shoal sites.

STUDY AREA AND METHODS

The York River estuary, a subestuary of the Virginia portion of the Chesapeake Bay (Fig. 1), covers about 208 km^2 and extends 46 km from Tue Marsh Light to West Point, where it is formed by the confluence of the Pamunkey and Mattaponi Rivers. At two localities within the estuary, tidal creeks similar in physical dimensions (O'Neil 1983), but differing in salinity regimes, were selected as study sites: Goalders Creek, a meso-oligohaline site (sensu Remane 1934 and the Venice System of classification), and Blevins Creek, a polyhaline creek in the Guinea Marshes near the mouth of the river (Fig. 1).

Field Methods

Within each locality three stations were established: 1) in each creek approximately 1,500-2,000 m upstream (where trawling was still possible), 2) immediately inside the creek mouth, and 3) at shoal stations positioned approximately 200 m offshore in the York River proper in approximately 3 m of water.

Monthly collections (March-October 1982) with a 4.9 m semiballoon otter trawl with wings and body of 19 mm mesh and a 6.3 mm mesh cod end liner were made during daylight hours as close to high tide as possible. Four 2-min tows at about 1 m s^{-1} were made at each station.

To reduce the chances of regurgitation, specimens were initially anesthetized in a mixture of seawater and 0.02 mL quinaldine (mixed in 10 mL acetone). Buffered formalin (10%) was then added for preservation. The abdominal cavities of large fish (>80 mm) were pierced to allow sufficient preservation of food items in the stomach. Water temperature and salinity were recorded prior to trawling at each station.

Laboratory Methods

In the laboratory, spot from each collection were sorted and counted. Individual standard lengths (SL) were measured; when more than 50 spot were captured in a single collection, a random subsample of 30 fish was used for length measurements.

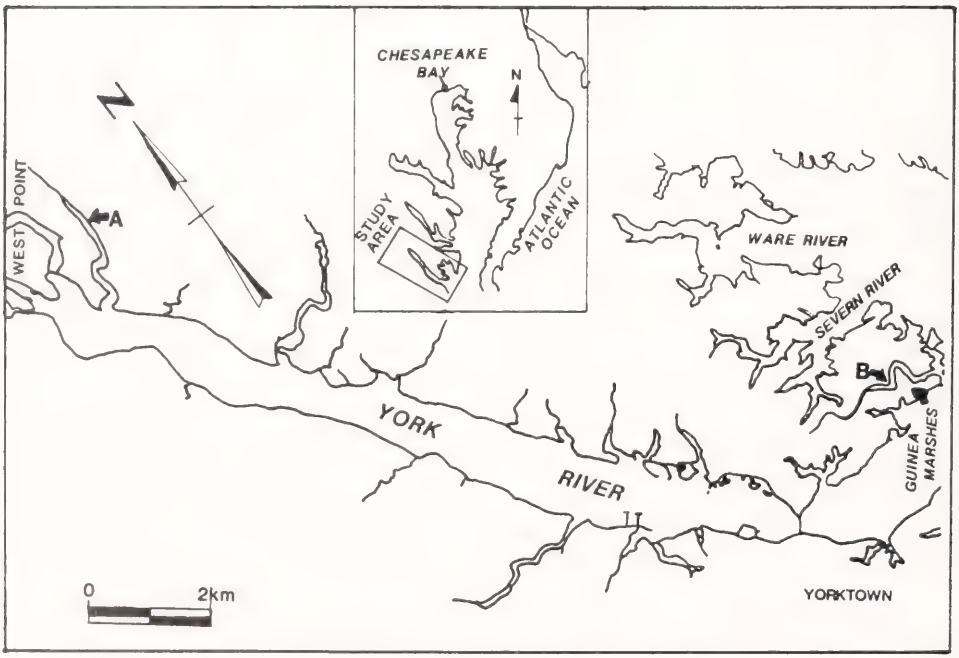

FIGURE 1.—York River, VA, and relative locations of tidal creeks examined. A = Goalders Creek, B = Blevins Creek.

For gut content analysis, fish from each of the four trawl samples representing a given station were pooled and then divided into several size classes. Initially, 5 mm size increments were used in order to corroborate the findings of others concerning an ontongenetic shift in feeding habits of spot. When mean standard lengths exceeded 20 mm, 10 mm size classes were adopted.

Initially, up to 20 stomachs were removed from randomly selected individuals in each size class. Later, based on prey item diversity (Hurtubia 1973) comparisons for the June samples, 12 stomachs per size class was set as the upper limit (O'Neil 1983).

Stomach contents were pooled within size classes and analyzed using the Carr and Adams (1972) sieve fraction technique. After washing stomach contents from each sieve (2, 0.85, 0.425, 0.25, 0.15, and 0.075 mm meshes) into a small fingerbowl, a random subsample of approximately 5 mL was removed. The subsample was placed in a labeled vial and the remainder was filtered onto a preweighed 55 mm filter pad and dried for 24 hours at 60°C. On the assumption that food particles of roughly the same size have approximately the same weight (Carr and Adams 1972), the total dry weight for each sieve fraction was proportioned among the prey types identified from its subsample. The Carr and Adams technique provided for rapid, accurate identification of food items from a large number of stomachs and has been used successfully by several investigators (Sheridan 1979; Stoner 1980; Livingston 1982; Lucas 1982).

Statistical Analysis

Dietary differences among various ontogenetic groups, between creeks, between stations within creeks, or for each month examined were compared using "normal" classification methods (Clifford and Stephenson 1975). Overlap of prey utilization was then determined using the complement of the Bray-Curtis dissimilarity measure:

$$\frac{\sum_{1}^{n} |x_{1_j} - x_{2_j}|}{\sum_{1}^{n} (x_{1_j} + x_{2_j})}$$

where n is the number of attributes (prey) and x_{1_j} and x_{2_j} are the values of the jth attribute for any pair of entities (size, station, month).

Separate matrices were constructed for each comparison from untransformed, pooled monthly data using COMPAH (Boesch 1977). The data in each matrix were then clustered by the group-average method (Lance and Williams 1967). Diet information was based on dry weights of the 30 prey taxa categories, all of which were mutually exclusive except for the unidentified (UID) and miscellaneous (MISC) categories (Table 1). Prey items contributing <0.1 mg of total dry weight per size class were eliminated prior to the analysis. The miscellaneous category contains the total of all food items individually representing <2% of the final dry weight.

In addition to the clustering procedure, reciprocal averaging ordination (Guinochet 1973; Hill 1973) was used to provide independent verifica-

TABLE 1.—Prey categories used for tropic comparisons. All but unidentified (UID) and miscellaneous (MISC) are mutually exclusive feeding categories.

AMP	Amphipoda
BIV	Bivalves
BRA	Branchipoda
CAL	Calanoids
CAP	Caprellidae
CLS	Clam siphons
CHI	Chironomidae
CHL	Chlorophyta
COR	Corophiidae
Crs	*Crangon septemspinosa*
CRZ	Crab zoea
Cs	*Callinectes sapidus*
CYA	Cyathura
DET	Detritus
Eh	*Eteone heteropoda*
Et	*Edotea tribola*
FOR	Foraminifera
GAM	Gammaridae
HA_1	Harpacticoid 1
HA_2	Harpacticoid 2
La	*Leucon americanus*
Lp	*Leptocheirus plumulosus*
MAC	*Macoma* sp
MAL	Maldanidae
Me	*Monoculodes edwardsi*
MISC	Miscellaneous
Na	*Neomysis americana*
NEM	Nematoda
NER	Nereidae
OLI	Oligochaeta
OST	Ostracods
PAL	Palaemonidae
PI	*Polydora ligni*
PLA	Plant matter
POL	Polychaeta
SPI	Spionidae
TEL	Teleosteii
UID	Unidentified remains
XAN	Xanthidae

tion of the dendrogram results. Reciprocal averaging is an eigenanalysis that ordinates both food type and habitat (or size class) variables simultaneously and defines axes such that the variance of the scores on each axis is maximized. The first axis, therefore, represents the path of maximum variance, the second axis the next greatest, and so forth. This analysis was performed with ORDIFLEX (Gauch 1977).

RESULTS

Physical Parameters

With the exception of April and May, temperatures were slightly cooler at Blevins Creek than at Goalders Creek (Table 2). Salinity within Goalders Creek was reasonably stable considering its meso-oligohaline location (Table 2). Except for a brief period in spring, Blevins Creek was polyhaline during the period of spot residence (salinity range 18-22‰). Salinity in Goalders Creek was always at least 4‰ lower than Blevins Creek and reached a maximum difference of 14‰ during April. Such variations in tidal creeks is typical of the estuarine salinity gradient with distance from the head of the estuary (Weinstein 1979; Weinstein et al. 1980). There were no distinct salinity differences observed between either creek and its adjacent shoal station.

Temporal Abundance and Distribution

Monthly abundance and distribution patterns for spot in each creek system and adjacent shoals are shown in Figure 2. Overall, numbers of spot captured within the tidal creeks were similar, 2,355 versus 2,802 in Goalders and Blevins Creeks, respectively. Temporal distributions of spot within each locality were further compared by computing creek/shoal ratios.

Spot were not encountered during the first sampling trip during late March 1982, but postlarvae and juveniles appeared in small numbers in April. At that time, spot were more abundant at the shoal stations than in the creeks (creek/shoal ratio of 0.28 for Goalders and 0.16 at Blevins). Young-of-year spot reached their maximum abundance in May, with 1,047 specimens taken up-estuary at Goalders Creek and 2,110 individuals sampled from Blevins Creek. Spot at Goalders Creek were then more numerous at the stations within the creek (ratio 20.5), but still more prevalent on the shoal down-estuary at Blevins Creek (ratio 0.52). From June to September, however, spot were clearly more abundant in the creeks of both systems. By the end of the investigation (October 1982) spot once again dominated the shoal at Blevins Creek, but remained more abundant in the creek at Goalders.

Monthly size distributions of spot in the two tidal creeks and adjacent shoals were examined by dividing the samples taken at each station into 5 mm SL size classes and comparing their relative frequencies among stations and locations. With the exception of a short period during recruitment (May) when more small fish were collected in Goalders Creek than at the nearby shoal station, none of the size-frequency comparisons differed significantly (Friedman's ANOVA, $P < 0.05$; O'Neil 1983).

TABLE 2.—Monthly temperature (°C), salinity (‰), and values and sediment analysis (% total dry weight) by trawl station, York River estuary, 1982.

Month	Goalders Creek			Blevins Creek		
	Upstream	Downstream	Shoal	Upstream	Downstream	Shoal
Mar.	11.0 (2.0)	11.0 (2.0)	11.0 (2.0)	9.5 (16.0)	9.5 (16.0)	
Apr.	13.5 (5.0)	13.5 (5.0)	15.0 (7.5)	16.0 (18.0)	16.0 (18.0)	17.0 (19.0)
May	20.5 (10.0)	20.0 (10.0)	21.0 (11.0)	24.0 (16.0)	24.0 (20.0)	24.0 (18.0)
June	26.0 (7.0)	26.0 (7.0)	26.0 (8.0)	25.5 (20.0)	25.0 (19.0)	25.0 (18.0)
July	29.0 (10.0)	29.0 (13.0)	29.0 (13.0)	28.0 (22.0)	28.0 (20.0)	29.0 (22.0)
Aug.	28.0 (11.0)	28.0 (11.5)	28.5 (10.0)	27.0 (22.0)	27.0 (19.5)	27.0 (20.0)
Sept.	26.0 (13.0)	26.0 (14.5)	26.0 (16.0)	25.0 (21.0)	26.0 (21.0)	25.0 (20.0)
Oct.	16.5 (11.0)	17.0 (11.0)	17.0 (12.0)	14.0 (20.0)	14.5 (22.0)	15.0 (20.0)
Sediments	(Sample cores taken in May)					
Sand and gravel	83.45	29.86	11.06	52.21	59.07	93.07
Silt	7.72	27.29	43.87	33.83	27.92	3.05
Clay	8.83	42.85	45.07	13.96	13.01	3.83
Organics	9.12	15.96	10.79	4.09	5.16	0.74

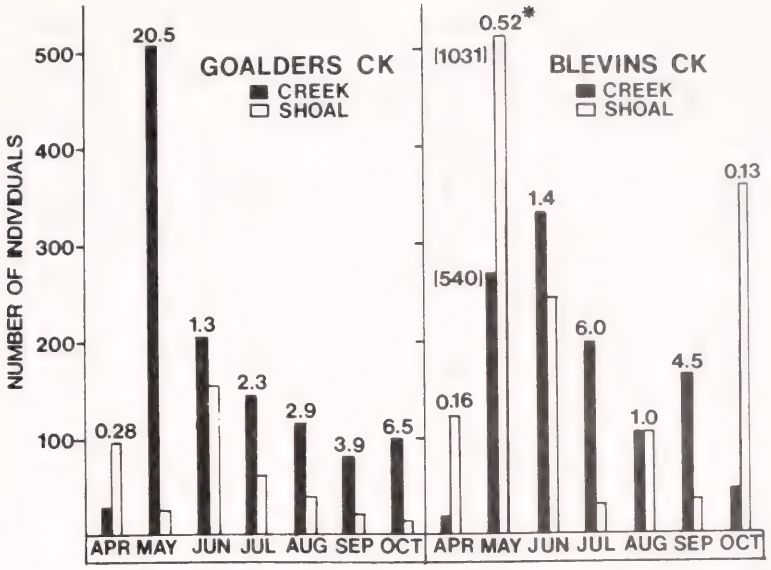

FIGURE 2.—Relative densities of spot at tidal creeks (values shown are monthly means of both creek stations) and shoal sampling localities. Asterisk indicates that May values for Blevins Creek are drawn to half scale. Values above histograms are ratios of creek to shoal densities.

Trophic Analysis

During this study, over 1,750 spot stomachs were removed and analyzed. In both creeks, spot underwent size-related, as well as temporal and spatial, changes in food utilization. Food utilization differences owing to size-related (ontogenetic) changes were examined by cluster analysis (Fig. 3). Calanoid copepods were the dominant prey of the smallest spot size classes (Fig. 4). The 26-30 mm size class had begun to consume more substrate-oriented prey (polychaetes and nematodes). All the spot examined between 40 and 100 mm SL had considerable overlap in a wide variety of food items. The great majority, however, were benthic organisms, e.g., maldanid and nereid polychaetes, *Leptocheirus* amphipods, free-living nematodes, and oligochaetes. Spot over 101 mm were clustered separately because of *Leucon americanus* in the diet. It thus appears that ontogenetic changes in spot diet shifted from a specialist mode when small to a more opportunistic strategy in larger size classes.

Size-class data were also subjected to reciprocal averaging ordination (Fig. 4). Results closely parallel those in the numerical classification. Axis 1, accounting for 49% of the variance, defined the small, planktonic size classes, which consumed mostly calanoid copepods. The spot over 101 mm were separated along Axis 2, with *Leucon americanus* and *Monoculodes edwardsi* the dominant food items. The remaining size classes lay in the plane of Axes 2 and 3 in association with a large variety of benthic prey.

The dendrogram representing the differences between stations for all size classes of spot pooled (Fig. 5) indicated that there are two main clusters that correspond to the food distinctions between the two creeks. In addition, both shoal stations clustered as distinct outliers.

Dominant prey items at the Goalders Creek sites included nereid polychaetes, clam siphons, a gammarid amphipod (*Leptocheirus plumulosus*), and harpacticoid copepods. At Blevins Creek, spot utilized proportionately more nematodes, maldanid polychaetes, and oligochaetes. At both locations spot made significant use only of specific parts of some prey items, i.e., clam siphons and tails of maldanid polychaetes (Currin et al. 1984).

Prey utilization differences were also noted between the creek stations and the adjacent shoal. At Goalders Creek the amphipod *Monoculodes edwardsi*, which dominated feeding on the shoal, was partially responsible for the separation noted in the dendrogram (Fig. 5). In the polyhaline sys-

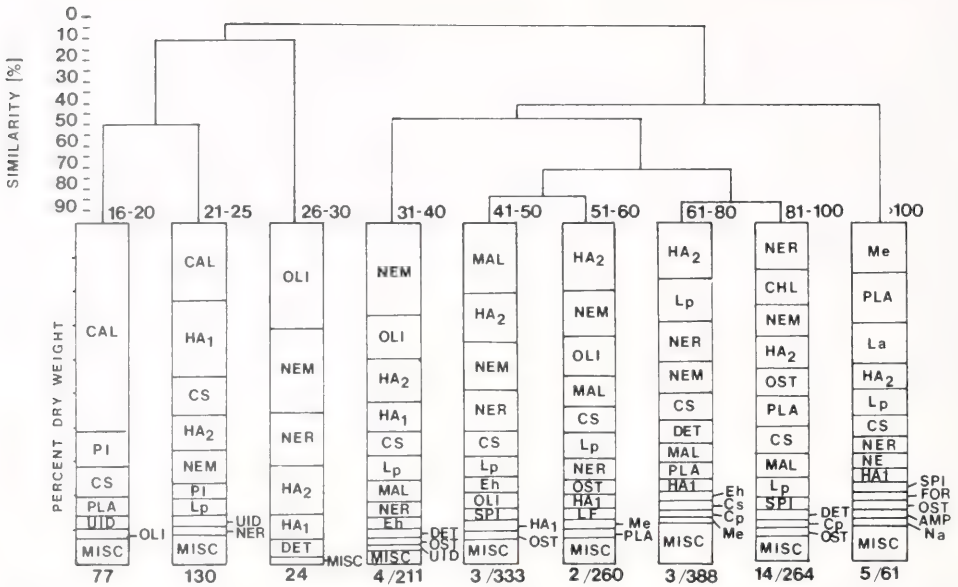

FIGURE 3.—Cluster analysis of prey similarity among *Leiostomus* size classes for the York River estuary, 1982. Prey abbreviations are listed in Table 1. Ratios at bottom of each column represent number of empty stomachs/ total sample size.

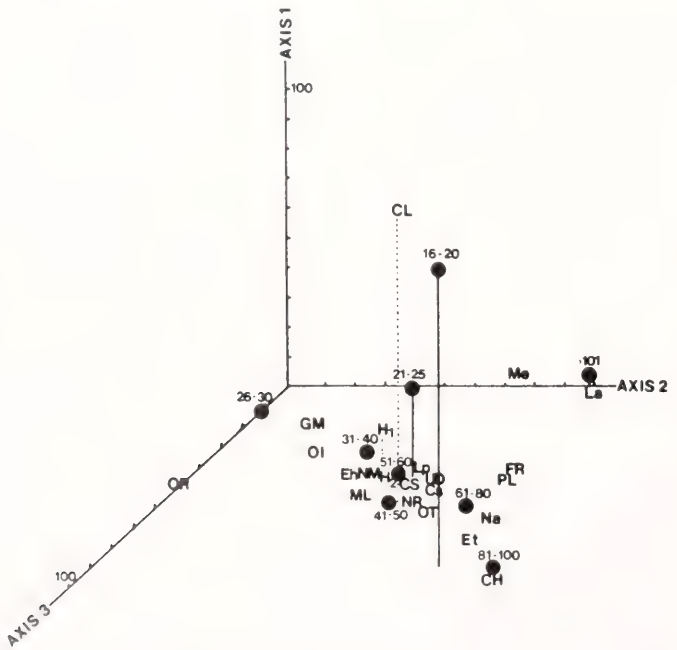

FIGURE 4.—Reciprocal averaging of prey and spot size class. Prey abbreviations: CH = Chlorophyta, CL = Calanoid copepods, Cs = *Crangon septemspinosa*, Eh = *Eteone heteropoda*, Et = *Edotea triloba*, FR = Foraminifera, GM = Gammaridae, H_1 = Small harpacticoid copepods, H_2 = Large harpacticoid copepods, La = *Leucon americanus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, Na = *Neomysis americana*, OL = Oligochaeta, OR = Orbiniidae, OT = Ostracods, PL = Plant matter.

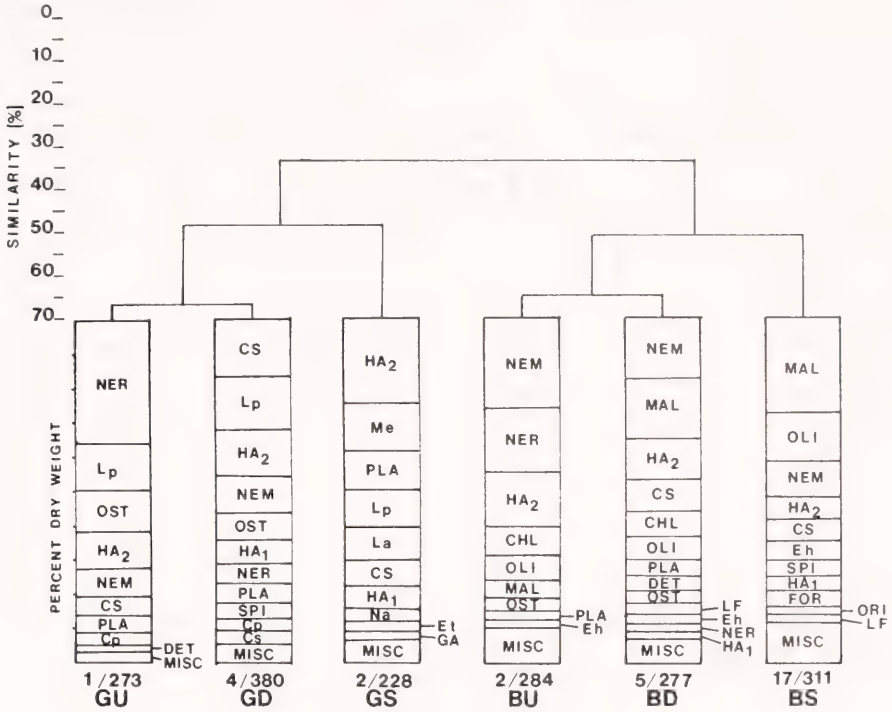

FIGURE 5.—Cluster analysis of prey similarity among habitats for spot from a polyhaline (BD = Blevins downstream, BU = creek, VA, 1982. Prey abbreviations are listed in Blevins upstream, BS = Blevins shoal) and a meso-oligohaline (GU = Goalders upstream, etc.) tidal Table 1. Ratios at the bottoms of each column represent number of empty stomachs/total sample.

tem, however, there were few clear differences caused by presence or absence of particular prey types. Instead, it was more a question of which food item was dominant. Spot appeared to eat more nematodes within the creek and more maldanid polychaetes on the shoal.

To confirm the results of the classification analysis, reciprocal averaging was used on the same food-habitat matrix (Fig. 6). Prey items located near a given station "lollipop" are the dominant food items utilized by spot at that station. Axis 1, accounting for 45% of the data variance, clearly separated the low and high salinity creek systems. Axis 2 (28% of the variance) isolated the shoal stations relative to the intracreek sites. Nematodes and maldanid polychaetes were again closely associated with the Blevins Creek sites. Nereids, *Leptocheirus*, and *Monoculodes* were dominant at the Goalders Creek habitats.

To compare seasonal patterns in food utilization between habitats, classification dendrograms were also constructed using monthly data for each creek (Figs. 7, 8). At Goalders Creek there was little overlap of prey utilized in April compared to all other months (Fig. 7). The main reason for this appears to be the large proportion of calanoid copepods consumed in April. August and October were grouped together because of the amount of nereids eaten, and the remaining months were added to this cluster individually, depending on their overall dissimilarity.

April was also an outlier at Blevins Creek, because of the dominance of calanoids in the diet of young spot (Fig. 8). May and June were clustered together because of the similarity in the consumption of maldanid polychaetes and nematodes. August and September were similar in the proportions of four prey items utilized: maldanids, nematodes, nereids, and harpacticoid copepods. Although these food items were probably incidental in their diet, July was a separate group because of the large amount of Chlorophyta present in the stomachs examined from that month; October was isolated because Foraminifera became an important addition to the diet.

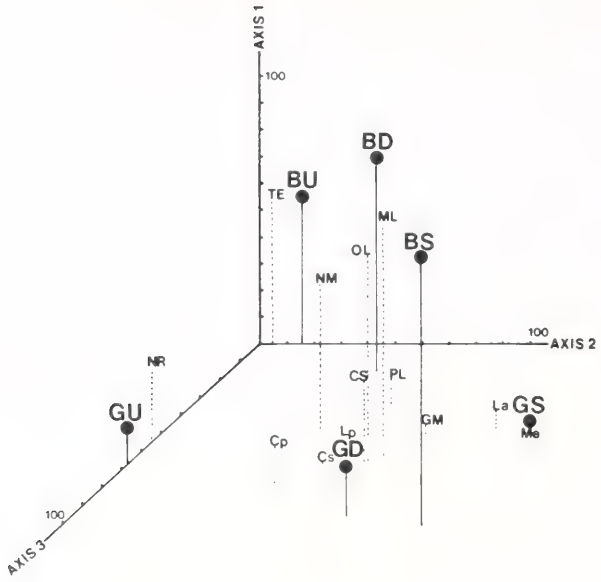

FIGURE 6.—Reciprocal averaging of prey and habitat for spot collected from tidal creeks and adjacent shoals of the York River, VA, 1982. Station abbreviations are the same as Figure 4. Prey abbreviations: Cp = *Cyathura polita*, CS = Clam Siphons, Cs = *Crangon septemspinosa*, GM = Gammaridae, Lp = *Leptocheirus plumulosus*, Me = *Monoculodes edwardsi*, ML = Maldanidae, NM = Nematoda, NR = Nereidae, OL = Oligochaeta, PL = Plant Matter, TE = Teleostei.

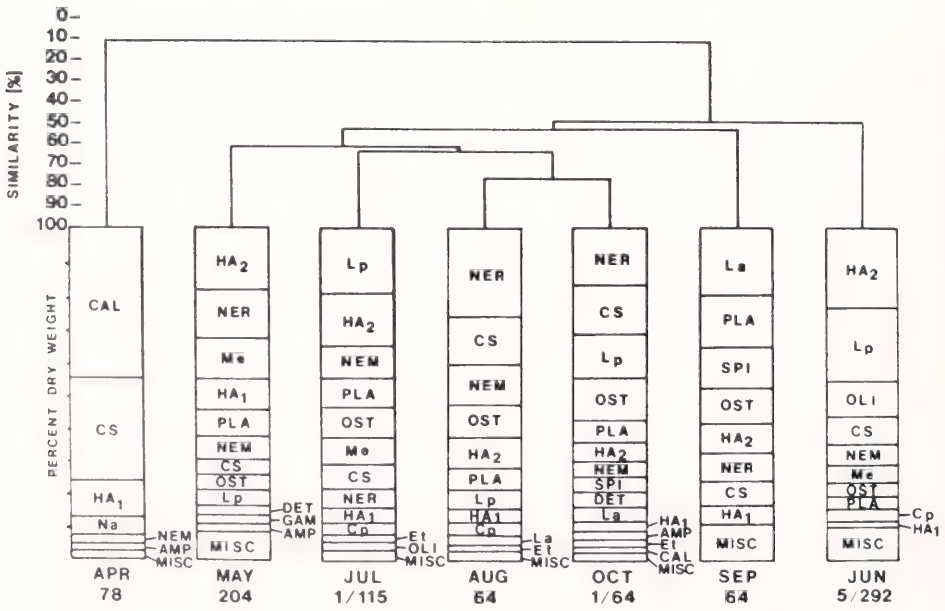

FIGURE 7.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Goalders Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at the base of each column represent number of empty stomachs to total sample size.

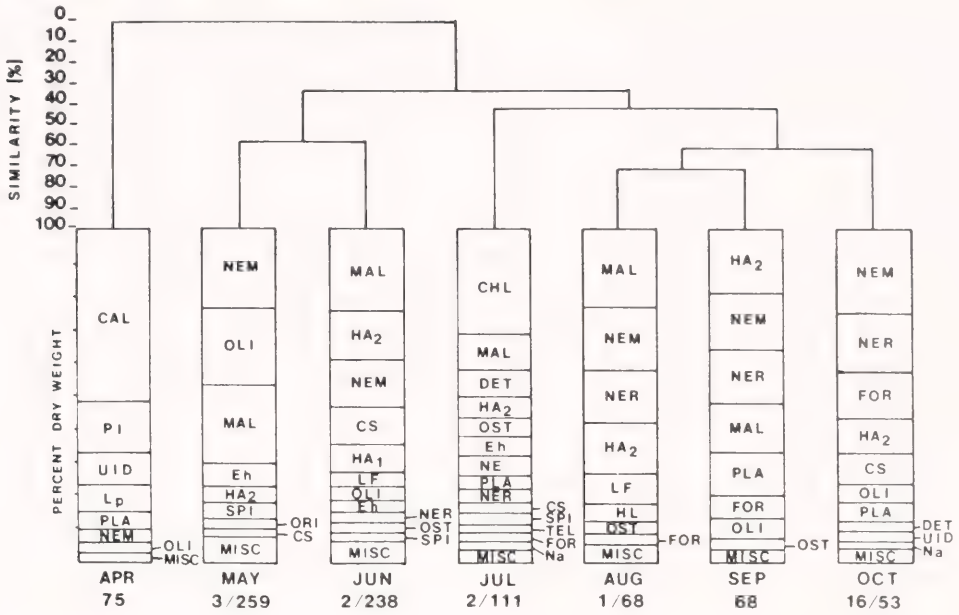

FIGURE 8.—Cluster analysis of monthly differences in prey utilization for young-of-year spot at Blevins Creek, VA, 1982. Prey abbreviations listed in Table 1. Ratios at base of each column represent number of empty stomachs/total sample.

DISCUSSION

As Livingston (1982) stated, "While food habits of fishes have been studied extensively, specific relationships of trophic interactions, habitat partitioning, and spatial/temporal variability of coastal fishes remain largely undetermined." While a more comprehensive understanding of these processes awaits properly designed experiments and hypothesis testing, several common patterns have begun to emerge. Despite the apparent abundant resources of the estuary as a whole, there seems to be a consistent "tracking" (among species) of these resources, reminiscent of resource partitioning in other aquatic systems (e.g., coral reefs). Individual species distributions are probably controlled by physiological constraints, predation pressure, and the availability of food (or a combination of these factors). That this tracking process, if real, may result from periodic scarcity of food in estuaries was tentatively stated by Thayer et al. (1974) and only recently reinforced by the studies of Weisburg and Lotrich (1986). The latter authors used experimental techniques to demonstrate food limitation occurring in the mummichog *Fundulus heteroclitus*, among fishes perhaps the most "perfectly" adapted food generalist in the estuary.

We did not observe differences in relative fullness of spot stomachs between the two creek localities examined (O'Neil and Weinstein, unpubl. data). Therefore, suitable food appears to be readily available in both creeks. The types of prey utilized in each area, however, were different and generally followed the temporal and spatial distributions of the dominant macrobenthos in these creeks (Robert Diaz[4]). Spot apparently feed opportunistically on the available resources present in the tidal creeks and shoals at any one time and do well throughout the estuary. There were no differences in growth rates or condition of spot observed in the tidal creeks in our study (Weinstein and O'Neil[5]). Thus, from an energetics standpoint, spot seem able to achieve similar growth rates in different creeks (and corresponding salinity regimes).

Hodson et al. (1981) noted that individual stomachs of small spot captured in the Cape Fear estuary were typically dominated by a single food cat-

[4]Robert Diaz, Virginia Institute of Marine Science, Gloucester Point, VA 23062, pers. commun. July 1983.

[5]Weinstein, Michael P., and Steven P. O'Neil. manuscr. in prep. Virginia Institute of Marine Science, Gloucester Point, VA 23062.

egory. This was also observed in the present investigation. Individual stomachs from spot captured in the same sample were often found to contain thousands of harpacticoid copepods or were completely distended by half a dozen nereid polychaetes. Such observations reinforce the notion of opportunism and feeding activities related to the concentration and availability of prey.

Spot, as well as other estuarine sciaenids, undergo distinct ontogenetic changes in feeding mechanisms with increasing size (Chao 1976; Chao and Musick 1977; Govoni 1981). Postlarvae and small juveniles are characterized by large eyes and a terminal mouth. They prey on mainly pelagic calanoid copepods and other small plankton (Townsend 1956; Peters and Kjelson 1975; Kjelson et al. 1975; present study). April was an outlier in the seasonal dendrograms of Figures 6 and 7 because the majority of spot at that time were in the smallest size class in Figure 8 and fed on mainly calanoid copepods. Although Thayer et al. (1974) concluded that food for meroplanktonic life stages of estuarine fishes may be limiting, we observed no differences in feeding success between spot consuming plankton and those eating benthos.

At about 20 mm SL, spot become more benthic oriented, feeding on various epifauna and infauna (Livingston 1982; present study). Sheridan (1979) also noted a distinction in prey utilization of smaller spot (20-29 mm). In the habitats of Florida's Apalachicola Bay, however, he noted that individuals in this size class consumed more insect larvae and polychaetes than copepods. His larger size classes utilized more bivalves. The difference between his observations and those in our study may simply be due to the difference in prey availability at the various locations. It should also be noted that other studies on the food habits of spot failed to recognize any size-related differences (Roelofs 1954; Darnell 1958; Stickney et al. 1975; Chao and Musick 1977; Hodson et al. 1981). This is possibly due to the selective nature of the gear used. Large seines and trawls fail to sample small fish (Chao and Musick 1977), and block netting in the high marsh may select against large fish (Hodson et al. 1981).

The dominant prey items consumed by spot in each habitat, and the basis for intercreek and shoal versus creek differences observed during our study, are partly explained by distribution patterns of macrobenthic invertebrates reported by Boesch (1977) for the York River, VA. Although that study was conducted several years before ours, and were restricted to the river shoals and channels, there is a close parallel between the patterns Boesch described and the diet of spot from similar localities within the York River. Boesch described a group of species that were "characteristically abundant in salinities of 10-20‰ throughout the Chesapeake Bay system but were not usually as abundant in higher salinities except in shallow water habitats or following disturbances." He referred to them as euryhaline opportunists that were important dietary constituents of spot at both creeks in our study.

Most of the identifiable polychaetes encountered in spot stomachs were from this group, e.g., *Nereis succinea*, *Eteone heteropoda*, and *Paraprionospio pinnata* (Spionidae). The cumacean *Leucon americanus* also belongs to this group and together with the amphipod *Monoculodes edwardsi* was consumed in large quantities by spot on Goalders shoal (Fig. 8). *Monoculodes* is a member of the group Boesch described as estuarine endemics, which are most frequent in mesooligohaline areas. Down-estuary at Blevins Creek, the maldanid polychaetes, especially *Clymenella torquata*, figured prominently in spot diets and were determined to be most abundant in that vicinity by Boesch.

In another study, Boesch (1973) examined macrobenthic distributions as related to sediment composition and seasonality in Hampton Roads, VA. Those results give further insight to prey availability for the habitats and time periods described in the present study. Boesch (1973) found *Eteone heteropoda* more common in May and rare in August, but distributed over all sediment types in the areas of lower salinity. This species was commonly consumed by spot at Blevins Creek in May, June, and July (Fig. 7). Another polychaete, *Polydora ligni*, was common in stomachs from Blevins Creek only in April, and Boesch (1973) noted it was more abundant in the estuary between February and May. *Clymenella torquata*, also consumed at Blevins Creek, was less abundant seasonally but showed a preference for muddy-sand sites. This species was a dominant component in the diet of spot at the downstream and shoal stations, both of which had higher proportions of sand compared to the upstream station. Two polychaetes, *Nereis succinea* and *Paraprionospio pinnata* (Spionidae), were found by Boesch (1973) in sand-mud and mud-sand sediments, respectively, which generally characterized the Goalders upstream and downstream substrates, respectively (Table 2). Thus, it is likely

that spot feed on seasonally and spatially dominant prey types from the available array and that the observed differences between creeks and shoals simply reflect availability of dominant prey types. The diversity of food types in spot stomachs may also reflect the general strategy of the feeding opportunist, which is favored when 1) food densities are periodically low and there is a premium on the ability of the predator to take a range of prey, 2) the predator has a relatively long period to gain energy, and 3) prey densities fluctuate widely (Schoener 1969). These are characteristics of the marsh habitats that spot frequent as well as the general life history strategy of spot in terms of spawning season and residence period in the primary nurseries (Weinstein 1981; Weinstein and O'Neil 1986).

Finally, there is the question posed in the introduction to this paper, i.e., the relative role of these tidal creeks as feeding versus refuge zones. As suggested in the introduction and discussed above, there seeemed to be adequate food for growth of spot in tidal creeks and shoal areas, at least during the year of this study. This observation was confirmed in a separate effort using increments of daily growth observed in the otoliths of spot collected in Goalders and Blevins Creeks in 1983, and in the same two creeks plus a mesohaline creek (Kings Creek, also located in the York River system) in the following year 1984 (Weinstein and O'Neil fn. 5). Unfortunately, comparative data on the mortality of spot in different tidal creeks and other habitats are not readily available. Weinstein and Walters (1981) reported evidence of differences in spot mortality among creeks in different marshes of the Cape Fear River estuary. Mortality was significantly higher in the polyhaline marshes of the Cape Fear system in 1977, and although the mean value was highest in the same marshes in 1978, the overall variability of the data resulted in a nonsignificant difference among marshes. Mortality rates calculated for spot in the studies of Weinstein (in press) and Weinstein et al. (1984) in Little Monday Creek and Blevins Creek (located about 1 km apart) differed from the values reported for polyhaline creeks in the Cape Fear estuary 0.029 and 0.015/day versus 0.061 and 0.052/day, respectively. The difference in mortality rates calculated for the two studies lies partly in the age distribution sampled from each population (youngest age cohorts were not sampled in the York River), but this factor alone is not believed to account for all of the difference in the rates. The role of differential mortality in shaping the population dynamics of this species is clearly in need of further study.

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ASSESSMENT OF MORTALITY IN AN OFFSHORE POPULATION OF QUEEN CONCH, *STROMBUS GIGAS* L., IN SOUTHWEST PUERTO RICO

RICHARD S. APPELDOORN[1]

ABSTRACT

A Jolly-Seber multiple tag-recapture experiment was conducted for 2 years on a queen conch population offshore of La Parguera, Puerto Rico in order to estimate mortality rates. Over 2,000 individuals were tagged in 9 sampling periods spaced at 3-month intervals from August 1983 to August 1985. The occurrence of fishing in half the intervals allowed estimates to be made of both fishing and natural mortality rates. Fishing mortality averaged 1.14 over the study period. An upper limit of natural mortality including effects of emigration, was estimated to be 1.53. Assuming random diffusion, emigration was estimated and subtracted from the above yielding a corrected value of natural mortality of 1.05.

The queen conch, *Strombus gigas*, is one of the most valuable fishery resources of the Caribbean. Under heavy fishing pressure, stocks throughout the region have declined (Brownell and Stevely 1981), and the need for management has become increasingly obvious. Ideally, management decisions should be based on a firm understanding of queen conch biology, stock dynamics, and rates of exploitation. Estimates of natural and fishing mortality rates are fundamental to understanding the dynamics of exploited populations and are prerequisites of many stock assessment techniques, e.g., yield-per-recruit analysis (Beverton and Holt 1957).

All previous reports of natural mortality rate in queen conch populations have been made using only juveniles (Alcolado 1976; Baisre and Paez 1981; Wood and Olsen 1983; Berg 1976). There are two primary reasons for this: 1) populations where adult queen conch are not fished have not been studied or assessed, thus mortality estimates would include losses due to fishing as well as from natural causes; 2) estimates derived from length-frequency analysis cannot be made for adults because growth in length ceases at the onset of sexual maturity. These past estimates of natural mortality rate have all been high, ranging between 1.0 and 4.0, depending upon the age-group studied, except those of Wood and Olsen (1983) who reported values of 0.19 and 0.04 between ages 1 and 2 and ages 2 and 3, respectively. Thus, there is a dichotomy among reported values. Intuitively, it is difficult to predict whether high or low values of natural mortality rate should be expected. A low value of natural mortality rate, comparable to that of Wood and Olsen, might be expected for *S. gigas* because, in general, natural mortality is inversely related to size (Ursin 1967; Peterson and Wroblewski 1984; Blueweiss et al. 1978; Pauly 1980) and other large mollusks, from temperate areas, have typically low values of natural mortality. However, natural mortality should also be significantly related to temperature, both directly and through growth-rate mediated effects (Pauly 1979, 1980). Thus, higher values should be expected in tropical species. A casual literature review revealed only one estimate of natural mortality (M) in tropical mollusks for comparative purposes: $M = 3.66$ for the aplysiid gastropod *Dolabella auricularia* from the Philippines (Pauly and Calumpong 1984).

In the present study, rate of mortality was estimated for an offshore queen conch population spanning a wide size range and including both juveniles and adults. The Jolly-Seber multiple tag-recapture method was used. Separate estimates were made during periods of fishing and nonfishing, thus allowing partitioning of mortality into its fishing and natural components.

METHODS

The study area was located in southwest Puerto Rico, 7 km south of La Parguera (Fig. 1). The area has a uniform depth of 17 m and consists of a broad, patchy sand and macroalgal plain with oc-

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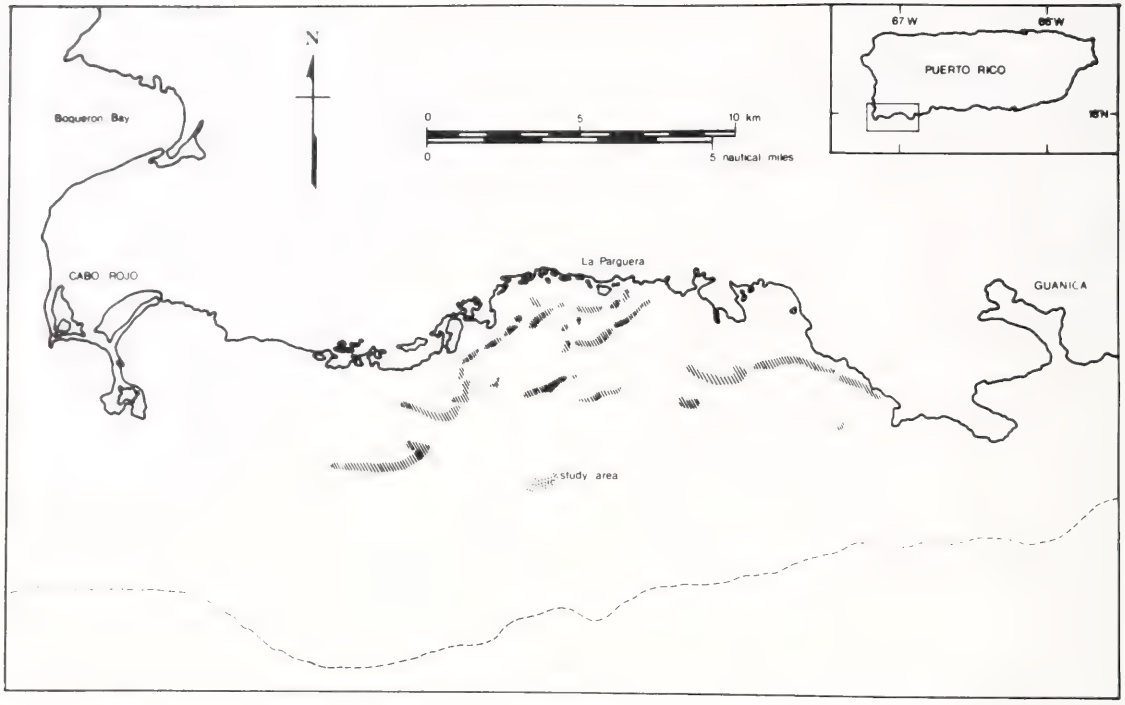

FIGURE 1.—Location of the queen conch study area (stippled) off La Parguera, Puerto Rico. Dashed line is the edge of the insular shelf. Shaded areas are emergent coral reefs.

casional patch reefs. The total study area is estimated to be 0.4 km^2, although for the first two periods sampling was limited to approximately the eastern 50% of the area.

Sampling occurred quarterly, generally in the latter half of August, November, February, and May, resulting in 9 sampling periods spanning 2 years from August 1983 to August 1985. Sampling during each period was conducted in the following manner. The area was surveyed by scuba divers and all data were collected in situ. Attempts were made to locate a minimum of 200 individuals. The maximum number was variable and subject to limits on queen conch density, the time dedicated to sampling (generally 3 weeks), and the weather during that time. During each period a two-stage haphazard sampling plan was used. Dive sites were located haphazardly throughout the full range of the study area, and the bottom covered during each dive was a function of direction and distance travelled, which also were determined haphazardly.

All queen conchs were tagged, when initially encountered, and measured for siphonal length to the nearest 1 mm using calipers. In addition, adults, defined by the presence of a flared shell-lip, were measured for lip-thickness in a similar manner. Tags consisted of 4.5 cm strips of Dymo[2] label tape, upon which a unique identification number was embossed. They were tied around the shell spire with nylon line (Fig. 2). The spines characteristic of queen conch shells held the tag firmly in place. Upon subsequent sightings tag number was recorded and shell dimensions remeasured.

During the 2-yr study period, casual assessments were made of fishing activity in the area. This was easy to do routinely as fishermen were willing to return tags from fished shells, and the presence of newly fished, empty shells on the bottom (left behind after meat extraction) was obvious after fishing had occurred. When encountered, tag numbers of these shells were recorded.

Data analysis used the Jolly-Seber method. The theory and practical mechanics of the method are presented in detail by Seber (1982: Section 5.1). It is valid for open populations where the effects of

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

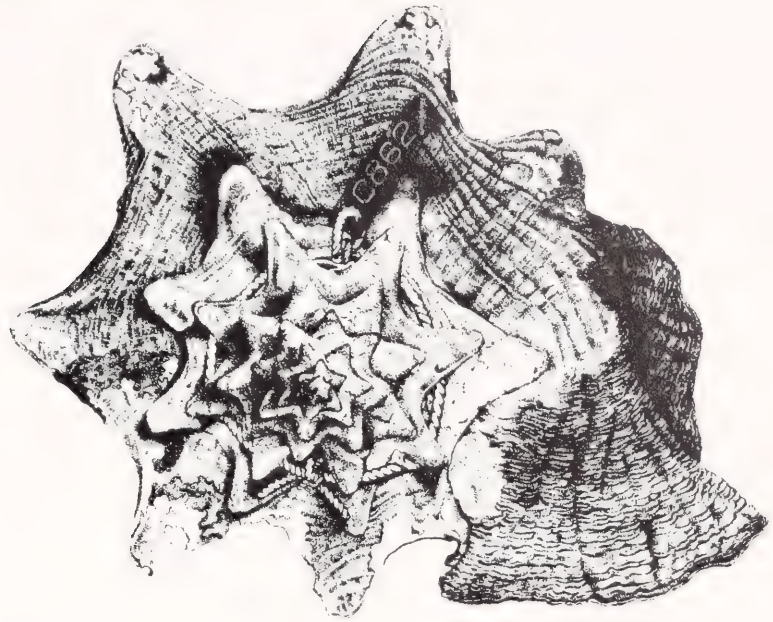

FIGURE 2.—Posterior view of adult *Strombus gigas* with numbered tag tied around the shell spire.

mortality, emigration, and recruitment can be significant between sampling periods. The assumptions of the method and their relation to the present sampling design are presented in the Discussion.

RESULTS

Over 2,000 individual queen conchs were tagged, spanning a range from 9 cm to 28 cm in length. Adult queen conchs averaged 24 cm in length and represented between 22% and 59% of sample populations, varying due to fishing activity and juvenile recruitment.

Tag return data are given in Tables 1 and 2 according to the methods in Seber (1982), with the results of the analysis given in Table 3. At any given time, roughly one-quarter of the population in the study area was tagged (Table 3, col. 2). Note the effect of increasing the sampling area at time 3 had on the estimate of abundance (N) at that time and on the estimates of survival (S) and

TABLE 1.—Tabulation of the number of queen conchs caught in the ith sample last caught in the hth sample (after Seber 1982). i and h designate sampling periods; n_i = number of conchs caught in the ith sample; R_i = number of conchs released at the ith sample; r_h = total number of conchs recaptured, last caught in the hth sample; m_i = number of conchs recaptured in the ith sample.

i	1	2	3	4	5	6	7	8	9	
n_i	424	196	275	228	352	375	262	231	227	Total
R_i	424	196	275	228	352	375	262	231	—	(r_h)
h										
1		42	28	19	22	8	1	0	0	120
2			18	7	17	6	0	0	0	48
3				10	9	2	0	2	0	23
4					40	14	5	1	1	61
5						76	22	3	2	103
6							37	13	4	54
7								35	22	57
8									36	36
m_i	0	42	46	36	88	106	65	54	65	

TABLE 2.—Tabulation of the number of queen conchs caught in the *i*th sample last caught in or before the *h*th sample (after Seber 1982). *i* and *h* designate sampling periods. z_i = number of different individuals caught before the *i*th sample which were not caught int he *i*th sample, but were caught subsequently, and is equal to the sum across the row excluding the diagonal element.

i	1	2	3	4	5	6	7	8	9	Total
h										
1		42	28	19	22	8	1	0	0	$z_2 = 78$
2			46	26	39	14	1	0	0	$z_3 = 80$
3				36	48	16	1	2	0	$z_4 = 67$
4					88	30	6	3	1	$z_5 = 40$
5						106	28	6	3	$z_6 = 37$
6							65	19	7	$z_7 = 26$
7								54	29	$z_8 = 29$
8									65	

TABLE 3.—Population estimates for queen conch derived from the Jolly-Seber multiple mark-recapture analysis. M/N = proportion of marked conchs in the population just before sample *i*; N = population abundance just before sample *i* with standard deviation $\hat{\sigma}[N/N]$ and coefficient of variation $\hat{\sigma}/N$; S = proportion surviving from the *i*th to $(i + 1)$ th sample with standard deviation $\hat{\sigma}[S]$ and coefficient of variation $\hat{\sigma}/S$; B = number of new individuals joining the population between the *i*th and $(i + 1)$ th sample with standard deviation $\hat{\sigma}[B]$ and coefficient of variation $\hat{\sigma}/B$.

i	M/N	N	$\hat{\sigma}[N/N]$	$\hat{\sigma}/N$	S	$\hat{\sigma}[S]$	$\hat{\sigma}/S$	B	$\hat{\sigma}[B]$	$\hat{\sigma}/B$
1	—	—	—	—	0.8387	0.1196	0.1426	—	—	—
2	0.214	1,629	310	0.1905	1.8956	0.4474	0.2360	2,585	1,017	0.393
3	0.167	5,673	1,437	0.2532	0.2372	0.0535	0.2257	409	324	0.792
4	0.158	1,754	341	0.1946	0.4706	0.0626	0.1330	62	148	2.398
5	0.250	888	106	0.1191	0.7359	0.1096	0.1490	608	136	0.223
6	0.283	1,261	196	0.1557	0.2913	0.0493	0.1692	361	89	0.246
7	0.248	729	117	0.1602	0.6208	0.1202	0.1937	542	152	0.280
8	0.234	995	205	0.2059	—	—	—	—	—	—
9	0.286	—	—	—	—	—	—	—	—	—

recruitment (B) between times 2 and 3. These figures are obviously unrealistic (e.g., survival cannot be greater than one) and are not considered in any subsequent analysis or discussion.

Survival rates of queen conch varied from 0.839 to 0.237 with coefficients of variation varying from 13.3% to 22.5%. Intensive fishing was known to have occurred in the study area between samples 3 and 4, and 6 and 7. Fishing also occurred between samples 7 and 8, but to a much lesser degree. In the former two periods estimated survival rates were the lowest found: 0.237 and 0.293, respectively. Survival estimates from all other periods represent the effects of only natural mortality and emigration. The average of these 3 values is 0.6817. This would correspond to an instantaneous rate of natural mortality per 3-mo period of 0.3832 $[= -\ln(1 - S)]$ if no emigration occurred. Assuming the effects of emigration are constant between sampling periods, estimates of instantaneous fishing mortality can be obtained by subtracting the average value of instantaneous natural mortality (which includes any emigration effect) from instantaneous total mortality for periods of known fishing activity. For sampling periods 3-4, 6-7, and 7-8, the instantaneous rates of fishing mortality per 3-mo period were, respectively, 1.056, 0.845, and 0.0935. Dividing the sum of these by the total time period for which mortality estimates are available (1.75 year) results in an estimate of the annual instantaneous fishing mortality rate (F) for the population in the study area of 1.14 between August 1983 and May 1985.

On an annual basis, the apparent instantaneous rate of natural mortality for queen conch is 1.533. However, this overestimates true natural mortality because permanent emigration was known to occur, and it was not possible to precisely quantify the effects of emigration on the basis of these data (see Discussion). The estimate does provide an upper bound on the value of natural mortality.

DISCUSSION

Model Assumptions

Principal assumptions of the Jolly-Seber method are that sampling is random, with catch-

ability equal for all individuals, that rates of survival are equal for all individuals, and that tag loss is negligible. No field study can hope to manipulate the environment to such a degree that all assumptions are perfectly met. Thus, potential deviations from these assumptions must be considered and their significance and resulting implications assessed (Begon 1983). Presented below is a review of each assumption. Based on known or suspected aspects of the biology and ecology of queen conch, potential problems with respect to each assumption are raised. Each potential problem is then considered in light of the specifics of the present study, and an attempt is made to assess its significance, if any. Finally, consideration is given to the robustness of Jolly-Seber estimates. In general, it will be shown that deviations from Jolly-Seber assumptions, if present, would be small and have little impact, and in addition, the Jolly-Seber method is robust to such deviations.

In the present study, sampling was conducted on an areal basis. Although sampling was not truly random (i.e., with areas predetermined in a random fashion), dive sites were spread throughout the study area and chosen without prior reference to, or knowledge of, the specific nature of the habitat or conch density in the immediate area. The two stage sampling design employed allowed every section of the study area to have an equal probability of being covered. The assumption of equal catchability is the more important property here, and there were several points where potential departures from this assumption could have arisen. Queen conchs usually showed a distinct clustered distribution. Within a cluster all individuals were felt to have an equal probability of capture, regardless of size. However, large queen conchs were easier to see at a distance. This would affect capture probabilities if distinct size groups characterized clusters; thus, clusters of large queen conchs would be noticed more frequently. While it was thought that there existed areas differentially characterized by the abundance of juveniles and adults, these areas generally occurred on a larger scale than typically covered on a dive. The random allocation of dive sites, then, should have minimized any effect of this heterogeneity. The tendency of very small queen conchs to remain buried is a second factor potentially affecting catchability. Thus, a small tagged queen conch (<13 cm) might have a reduced probability of recapture until it grows large enough to be exposed most of the time. However, only a very small fraction of queen conchs sampled would have been affected by this. By the time the animals are large enough to be sampled in significant numbers, they will, by the time of next sampling, have grown to a size where burial is not a problem; thus recapture would not be affected. In sum, for the size range sampled, it is thought that departures from the assumption of equal catchability are small, if present. Pollock and Mann (1983) and Carothers (1973) have both found Jolly-Seber estimates of survival to be robust against heterogeneity of capture probabilities.

Mortality of queen conch could have been dependent upon mark status if tags attracted predators. There is no direct evidence (e.g., observations or signs of predators or predation during tagging periods) to indicate that this problem occurred, implying that it did not. Tags quickly fouled with macroalgae and were subsequently impossible for divers to see at any distance. Thus, any tag attraction effect could only occur immediately after initial tagging. As such, the problem is thought to be negligible. Departures from equal probability of survival may have occurred owing to size related processes, but not to a serious degree. Natural mortality is thought to decrease with age, with the effect being predominant among small juveniles (Appeldoorn in press a, b). However, the majority of queen conchs sampled here were large juveniles and adults, which should have had similar survival probabilities. Although fishermen usually take all sizes of queen conchs found, large conchs should have suffered a greater mortality because generally fishermen will not dive in an area unless conchs are visible (i.e., large) from the surface or on shallow test dives. Thus, areas predominantly characterized by small queen conchs should have been undersampled by fishermen. Again, the potential effect of this is offset because the majority of conchs were large. Also, only a portion of the small queen conchs were from areas particularly characterized by such individuals. Lastly, rate of dispersion is also a function of size (Hesse 1979; Appeldoorn and Ballantine 1983), so the emigration component of survival could have been higher for larger individuals. This, to some degree, would counter the size-mortality trend, with the effect being predominant among small juveniles. As such, the effect here should also have been minor. In sum, there is no reason to suspect substantial departures from the assumption of equal probability of survival, and if survival is independent of mark status and probability of

capture is independent of age, Jolly-Seber survival estimates are not greatly affected by age-dependent mortality (Seber 1982).

There are methods available for determining age-dependent mortality rates from Jolly-Seber data (Pollock 1981; Pollock and Mann 1983). Queen conchs, however, are difficult to age (Appeldoorn 1987). Length groups could be used, but these would have to be defined narrowly so that all individuals could grow into the next largest size group within the 3 months between sampling periods, thereby reducing sample sizes within length groups to impractical levels. Data pooled over time would have forced confounding of natural and fishing mortality effects, which was deemed undesirable.

Tags were held securely in place because spines on the queen conch shell spire prevented tie lines from slipping off, and they became more secure over time due to fouling. Numbers remained readable throughout the 2-yr period. In only those individuals with poor spine development could the tag be lost, and then only within the short time prior to fouling. These included some very small juveniles (<12 cm) and a few very old queen conchs where spines had been eroded. The total number of such potential cases was exceedingly small and is, therefore considered negligible.

Estimation of Emigration and Natural Mortality

Permanent emigration of queen conch was known to occur. Reports from fishermen placed some individuals as much as 9 km away from the study area, although the time this took is unknown. The degree of emigration needs to be accounted for if a more accurate estimate of natural mortality is to be obtained. Emigration can occur by either of two dispersion processes: random diffusion, and directed migration or drift. Seasonal migrations are expected in late fall and early spring based on other studies (Hesse 1979; Appeldoorn 1985), although the expected distance travelled is unknown. However, no evidence of such migration is apparent in the data for either mortality or recruitment. Possible reasons for this are 1) the mortality component is confounded by fishing effects thereby masking seasonal trends, 2) Jolly-Seber estimates of B are typically imprecise (Seber 1982), and 3) sampling periods were too few and inopportunely placed. Since the data do not support the occurrence of significant drift, at least to the point where it can be partitioned from diffusion, the degree of emigration was estimated by analyzing diffusion only.

Skellam (1951) presented a two-dimensional diffusion model which can predict the proportion of a population (P_t) outside the area of radius (ρ_t) in a given time (t) if the average distance travelled (ϵ) per unit time (Δt) is known. Assuming no mortality or birth, the equation is

$$P_t = \exp[-(\rho_t{}^2)/(t \cdot \epsilon^2/\Delta t)]$$

To estimate emigration an average value of ϵ is needed. Dispersal ability in *Strombus* is related to size (Hesse 1979; Miller 1972; Appeldoorn and Ballantine 1983). Specifically, if total movement is expressed solely as diffusion, the data of Hesse (1979) from a 1.5-mo period encompassing episodes of both diffusion and drift indicated that adults travelled twice as fast as "maturing" queen conchs (adults with thin lips or very large juveniles) and three times as fast as juveniles. Hesse (1979) recorded adults to move commonly 50-100 m/day, but no average figure was given, and it is assumed that rates less than this were also common. Clifton et al. (1970) tracked one group of adult queen conchs at 45-55 m/day over several days. Given these rates, a value of 50 m/day seems a reasonable estimate of ϵ for adults, averaging higher values during migration with lower values at other times. The La Parguera population consists of both juveniles and adults, so this value needs to be adjusted downward accordingly. Since the majority of queen conchs were old juveniles or young adults, an average stage of "maturing" can be assumeed, and a value of ϵ, one half that for adults, would be most appropriate, i.e., ϵ = 25 m/day. If it is assumed that the 0.4 km^2 study area is a circle of radius ca. 350 m, then in one sampling period (90 days) 11.2% of the population would be expected to emigrate. This results in an instantaneous rate of annual emigration equal to 0.481. Subtracting this from the estimate of natural mortality plus emigration (1.533) yields a corrected estimate of natural mortality rate at 1.05.

This value of natural mortality rate is lower, but consistent with values reported by Alcolado (1976), Berg (1976), and Baisre and Paez (1981), which might be expected since their estimates were limited to juveniles. However, it is still much greater than those reported by Wood and Olsen (1983). Hoenig (1983) presented empirical equations predicting mortality rate on the basis of oldest known age, which can be used for com-

parative purposes. Given a maximum life span of 7 years (Wefer and Killingley 1980) the predicted mortality rate is 0.72, a result compatible with the above estimate of natural mortality rate considering the variability associated with each estimate.

Status of the Fishery

The value of fishing mortality (F) relative to natural mortality (M) indicates that the La Parguera *S. gigas* population is intensely exploited. Gulland's (1971) calculation of $F = M$ at the point of maximum sustainable yield (MSY) would indicate, allowing for variability in the estimates, that the population was being fished at or above F_{MSY} at this time. However, Francis (1974) has shown that this relationship does not always hold, and Caddy and Csirke (1983) stated that tropical species in particular, already characterized by high levels of natural mortality, would be more likely to be overfished according to this formula. Using this conservative approach, a diagnosis of overfishing seems warranted. Since the study area is representative of that portion of the offshore La Parguera shelf supporting queen conch fishing, in terms of habitat, conch density, and general fishing activity, these results should have general relevance.

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POPULATIONS OF HORSESHOE CRABS, *LIMULUS POLYPHEMUS*, ON THE NORTHWESTERN ATLANTIC CONTINENTAL SHELF

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ABSTRACT

This report analyzes the distribution and abundance of horseshoe crabs, *Limulus polyphemus* (L.), on the Middle Atlantic continental shelf, based on Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys of the past two decades at depths beginning at 9 m. Crabs were collected from North Carolina to southern New England, with the highest abundance and frequency of occurrence between Virginia and New Jersey. Approximately 90% of the minimum estimated standing stock size in that area, 2.3-4.5 million individuals, was located at depths <30 m. The geographic distribution may reflect proximity of this shelf region to the principal spawning areas in Delaware and Chesapeake Bays. Seasonally, horseshoe crab abundance on the shelf declined during those months when spawning in estuaries peaked. Crabs were caught at depths to 290 m, the limit of sampling; most of the animals caught at depths >100 m were off Cape Hatteras, North Carolina. Despite the presence of horseshoe crabs in estuaries as far north as Maine, New York is the northward limit on the shelf. This suggests that inshore populations in New England may be relatively isolated from each other and from the large Middle Atlantic shelf population.

Generalizations about the natural history, behavior, and ecological importance of horseshoe crabs, *Limulus polyphemus* (L.), are primarily based on studies of the shallow-water phase of its life cycle (Shuster 1979, 1982; Wells et al. 1983). The populations in the mid-Atlantic region are most accessible in late spring and early summer, when adults spawn en masse on sandy estuarine beaches. Knowledge of behavior (Shuster 1950; Rudloe 1980; Barlow et al. 1982; Cohen and Brockmann 1983), orientation (Rudloe and Herrnkind 1976; Botton and Loveland in press), morphometrics (Shuster 1955; Riska 1981), sediment disturbance (Woodin 1978, 1981), and predation (Smith and Chin 1951; Smith et al. 1955; Botton 1984a, b) is all based on studies of shallow-water or intertidal individuals. Population estimates have been restricted to shallow-water adults (Baptist et al. 1957; Sokoloff 1978; Rudloe 1980; Shuster and Botton 1985), with the exception of Botton and Haskin (1984), who surveyed the population on the inshore New Jersey continental shelf.

Perhaps because of the spectacular intertidal mass spawning phenomenon and accessibility, estuarine populations have received a disproportionate amount of attention by ecologists. In contrast, most of the animal's life is spent sublittorally. An adult female may spawn completely over several successive high tides; in general, repeated breeding is more characteristic of males (Rudloe 1980). Juveniles, during their first and second summer, are abundant on intertidal flats (Shuster 1955, 1979), but the remainder of the species' 14-19 year life span (Ropes 1961) is spent subtidally except for the annual spawning migration.

This report summarizes latitudinal and bathymetric distributions of horseshoe crabs on the northwestern Atlantic continental shelf. Northeast Fisheries Center (NEFC) bottom trawl and ocean clam surveys during the past two decades have provided extensive data on the abundance and distribution of horseshoe crabs, principally north of Cape Hatteras, NC (Ropes et al. 1982; NEFC unpubl. data). Seasonal and annual trends in abundance are also discussed in the present report. Concern for evaluating the general population characteristics of horseshoe crabs parallels expanding commercial exploitation of the species. Animals are presently harvested to extract blood for the *Limulus* amoebocyte lysate (LAL) test, and as bait in eel (*Anguilla rostrata*), conch (*Busycon* sp.), and other fisheries (Pearson and Weary 1980); the vast majority of the fishing ef-

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fort is concentrated between Virginia and New Jersey (Botton and Ropes in press).

MATERIALS AND METHODS

NEFC bottom trawl surveys ranged from Cape Fear, NC, north to the Scotian Shelf; clam surveys cover the Middle Atlantic region north to Georges Bank. Both are general purpose survey programs, collecting data for standing stock assessments for many finfish and shellfish species, as well as collecting specimens for age determination, dietary analysis, and many other purposes (Grosslein 1969; Clark 1979).

During the period covered by this study (1975-83), the #36 and #41 Yankee otter trawls were used as sampling gear during bottom trawl surveys. Both nets have a mesh size of 5 inches throughout the wings and body, and 4.5 inches in the cod end. A liner of 0.5-in nylon mesh is employed at the aft end of the top belly and the cod end. Trawls are equipped with roller gear to facilitate use over rough bottoms. All tows were 30 minutes in duration at a vessel speed of 3.5 knots; stations were located using loran. An average of 1,129 stations per year was sampled (range, 711 stations in 1975 to 1,547 stations in 1979). Cruises were conducted during fall (September through early December) and spring (March through May) in all years, with five additional surveys during the summers (July through August) of 1977-81 and two during the winters (January through February) of 1978 and 1983. Sampling was conducted both day and night. After sorting the catch, personnel recorded the number of horseshoe crabs taken in each tow and their total wet weight to the nearest 0.1 kg.

A stratified random sampling design was used in the surveys (Grosslein 1969). The region was divided into several strata based primarily on depth. Stations were allocated to strata roughly in proportion to the area of each stratum and assigned to specific locations within strata at random (Clark 1979). For the purpose of this paper, stations of 9-27 m (5-15 fm) depth were defined as "inshore" and those deeper than 27 m as "offshore". Preliminary inspection of the catch data compiled by Ropes et al. (1982) showed the bulk of the horseshoe crab population to be located between northern New Jersey and southern Virginia. Within this region, there were 27 inshore and 16 offshore strata, based on depth and location. Stratified mean number per tow and biomass per tow of horseshoe crabs were converted into estimates of standing stock by using the "area swept" by a standard survey trawl in relation to catch as an estimate of minimum absolute density. Tows within strata were used to calculate variances around the means. Total populations for the inshore and offshore regions were estimated by expanding the average stratified mean catch per tow by the ratio of total area surveyed to the area sampled by an average tow. Further details of statistical methods are found in Clark (1979).

Ocean clam surveys used commercial style hydraulic dredges, towed for 5 minutes at 1.5 knots. The design and performance of this sampling gear is discussed by Meyer et al. (1981). Cruises from 1965 to 1978 used either a 30-in (91 cm) or 48-in (122 cm) knife-width dredge; cruises from 1979 to 1983 used a 60-in (152 cm) dredge. There were no ocean clam surveys in 1968, 1971-73, and 1975. Station locations were selected using a stratified random sampling design; the average number of stations sampled per year was 370 (range, 139 in

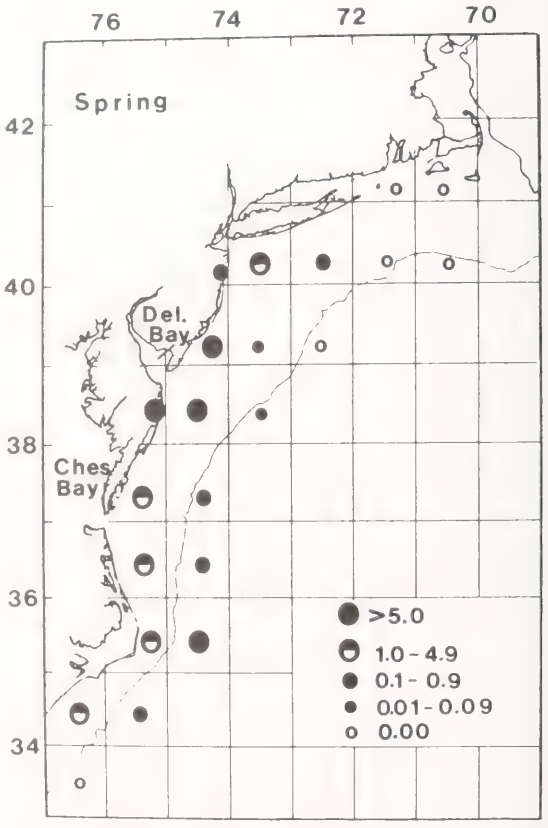

FIGURE 1.—Mean number of horseshoe crabs per tow,

1979 to 655 in 1966). Catches were not expanded into stock estimates, as for the bottom trawl survey data.

To analyze broad latitudinal variations in abundance and frequency of occurrence, catch and sampling effort were grouped by 1-degree latitude and longitude blocks. For example, stations at lat. 38°06′N, long. 74°02′W and 38°45′N, 74°50′W were both grouped together as 38°N, 74°W. Bottom trawl and ocean clam survey data were analyzed separately, because stratification schemes differed and the efficiencies of the two types of sampling gear cannot readily be compared.

RESULTS

Latitudinal Distribution

During groundfish surveys, 7,035 crabs were taken at 983 stations distributed from 33°N to 41°N; 75% of the crabs were caught between 37°N and 40°N (Fig. 1, App. Table 1). Highest abundance and frequency of occurrence was found on the shelf nearest the mouth of Delaware Bay. The maximum number of individuals per tow, 99, was obtained on 22 March 1976, from a station located off Assateague Island, VA, at 38°00′N, 75°14′W, in 13 m of water. Mean number per tow generally decreased with increasing distance from shore (Fig. 1).

Horseshoe crab abundance decreased both north of 40°N and south of 37°N (Fig. 1). Crabs were absent northeast of Montauk Point, Long Island (41°N, 72°W), and no crabs were found on or north of Georges Bank despite intensive sampling effort. Fewer than 2% of all horseshoe crabs collected were found south of 35°N (Cape Hatteras), and only one animal was caught south of 34°N.

The observed latitudinal distribution of horseshoe crabs in ocean clam surveys paralleled the above trends. A total of 1,640 animals was taken at 535 stations clustered primarily between Vir-

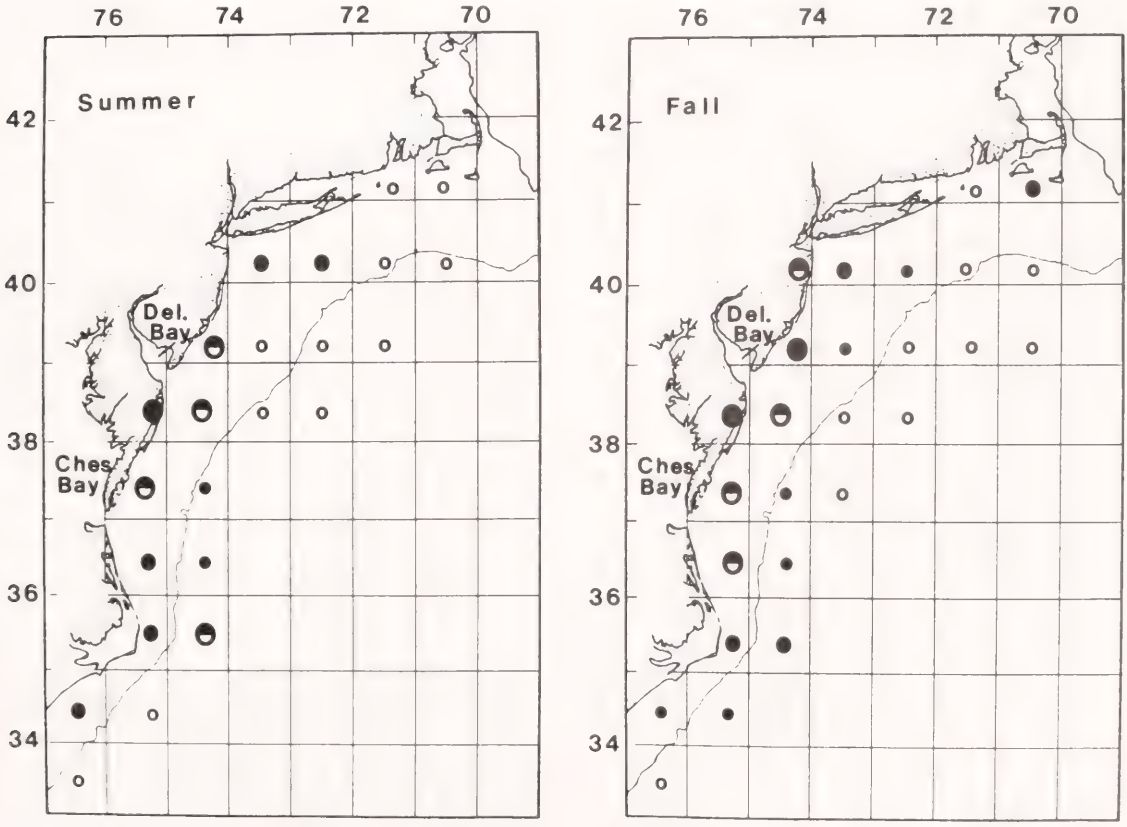

FIGURE 1.—*Continued*—by 1° latitude and longitude blocks, based on NEFC groundfish trawl data from 1975 to 1983.

TABLE 1.—Distribution of horseshoe crabs in clam surveys, 1965-83; 1,640 animals enumerated at 535 stations. Number of crabs over (number of stations with one or more individuals) in each row.

Latitude (N)	Longitude (W) 75°	74°	73°	72°
40°		4 (3)	23 (14)	4 (4)
39°		115 (46)	3 (3)	
38°	237 (77)	351 (103)		
37°	671 (176)	30 (16)		
36°	153 (76)	1 (1)		
35°	48 (16)			

ginia and New Jersey (Table 1). Thus, horseshoe crabs were most abundant along the continental shelf from Virginia to southern New Jersey in both groundfish and ocean clam surveys.

Seasonal and Annual Variations in Standing Stock

On the New Jersey-Virginia continental shelf, average abundance and biomass were highest during spring and fall cruises, lower in summer, and lower still (based on limited sampling) in winter (Fig. 1, Table 2). Horseshoe crabs were present in more than half the inshore tows throughout the year. Frequency of occurrence did not fluctuate as widely as abundance or biomass, and was consistently higher inshore than offshore.

Population estimates show considerable annual variation, with highest recorded catches in spring of 1976 and 1981 (Fig. 2). However, no clear trends in standing stock between 1975 and 1983 were evident. We estimate, based on the more complete fall and spring surveys, a minimum inshore population ranging from 1.8 to 3.1 million individuals (2,969 to 3,626 t), and a minimum offshore population ranging from 0.5 to 1.4 million individuals (972 to 1,975 t) (Table 2), for a total of some 2.3-4.5 million individuals. Coefficients of variation, based on individual stratum catches, ranged from 11.6 to 41.6 for individual inshore survey estimates, and from 23.6 to 87.5 for offshore estimates.

TABLE 2.—Average of seasonal variation in horseshoe crab abundance and biomass on the continental shelf, northern New Jersey to southern Virginia, based on groundfish surveys from 1975 to 1983. Strata shallower than 27 m were defined as inshore, and strata deeper than 27 m were defined as offshore.

	Winter	Spring	Summer	Fall
Inshore				
Mean no. per trawl	0.41	7.44	3.26	4.54
% occurrence	56	76	61	78
Population ($\times 10^6$)	0.410	3.103	1.258	1.881
Biomass (metric tons)	93	3,626	2,075	2,969
Offshore				
Mean no. per trawl	—	1.03	0.10	0.42
% occurrence	—	29	30	22
Population ($\times 10^6$)	—	1.445	0.129	0.530
Biomass (metric tons)	—	1,975	231	972

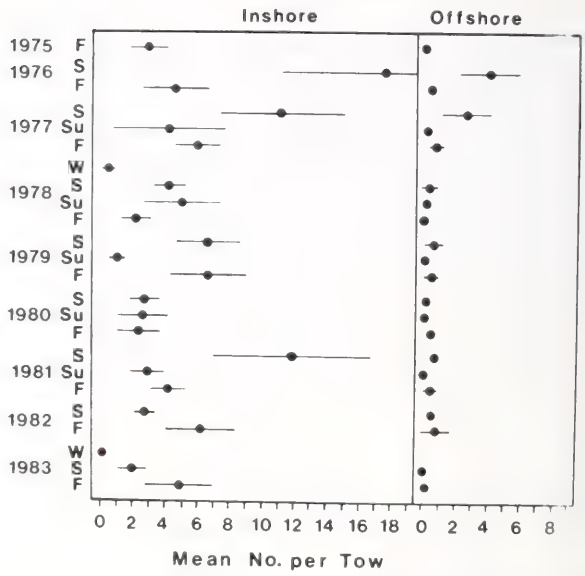

FIGURE 2.—Mean number of horseshoe crabs per tow (with 95% confidence limits) on the continental shelf from New Jersey to Virginia, based on NEFC groundfish trawl data from 1975 to 1983. W = winter; S = spring; Su = summer; F = fall; Inshore = all tows within sampling strata shallower than 27 m; Offshore = all tows within sampling strata deeper than 27 m. Where no confidence limit is shown, calculated limit was smaller than the width of the datum point.

Bathymetric Distribution

Horseshoe crabs were taken at stations between the inshore sampling limit, 9 m, and 290 m depth (Fig. 3). Seventy-four percent of the total number caught in bottom trawl surveys were taken from stations shallower than 20 m; and 92% were caught at depths <30 m. This trend was not an artifact of sampling effort. Offshore stations (>27 m) comprised approximately 73% of the sampling effort but produced <10% of the

catch. Mean abundance and biomass were nearly an order of magnitude higher at the inshore strata than the offshore strata, and horseshoe crabs were at least twice as likely to be caught inshore than offshore during all seasons (Table 2). The operation of the hydraulic clam dredge was limited to waters <80 m, and within this range, crabs were again most abundant at shallower depths. Sixty-two percent of the total catch was found shallower than 20 m, and 90% was found shallower than 30 m (Fig. 3).

Ninety-six animals were caught in 19 tows from 100 to 199 m depth, while 53 animals were taken in 7 tows below 200 m (Table 3). These deep-water individuals were caught between 34°21′N and 37°42′N (North Carolina to southern Virginia), with the majority from Cape Hatteras, south.

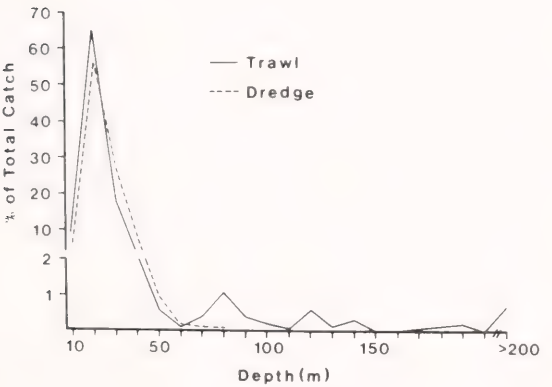

FIGURE 3.—Bathymetric distribution of horseshoe crabs, as percent of total catch, based on bottom trawl data (solid line) and ocean clam dredge data (dashed line).

DISCUSSION

Horseshoe crabs on the northwestern Atlantic continental shelf were most abundant between Virginia and New Jersey. On this section of the shelf, the population was estimated to be some 2.3-4.5 million individuals and was relatively constant between 1975 and 1983. The estimate of inshore abundance was necessarily conservative, because large survey vessels could not operate in shallow water. Horseshoe crabs may be abundant in areas inshore of the NEFC surveys; for example, in New Jersey State surveys, stations <1.8 km from shore frequently have over 10 horseshoe crabs/5-min hydraulic dredge tow in the Cape May area (Botton and Haskin 1984), and in areas of Narragansett Bay, 20-min otter trawls conducted by the State of Rhode Island have caught up to 40 horseshoe crabs (R. Sisson[3]). Both inshore and offshore stock estimates may also be conservative because the trawls, which are equipped with roller gear, may be <100% efficient in sampling horseshoe crabs, particularly if the animals are burrowed.

Seasonal surveys of the middle Atlantic continental shelf indicate a decline in horseshoe crab abundance during summer (July-August), which is consistent with the hypothesis that the shelf animals have seasonal inshore spawning migrations (Shuster and Botton 1985). More animals were caught during spring (April-early May) and fall (September-early December) periods, representing the prespawning and postspawning seasons, respectively. Therefore, the Virginia to New Jersey shelf population probably consist largely of individuals which spawn during the spring and early summer in the Chesapeake and Delaware Bays, and disperse offshore.

The range of horseshoe crabs on the continental

[3]R. Sisson, Division of Fish and Wildlife, Rhode Island Department of Environmental Management, Wakefield, RI 02879, pers. commun. December 1983.

TABLE 3.—Occurrence of all horseshoe crabs below 100 m depth on the continental shelf in groundfish surveys from 1975 to 1983.

Depth (m)	Latitude (N)	Longitude (W)	Date	Number of crabs
102	34°25′	75°53′	3/79	1
113	35°29′	74°50′	3/82	25
117	35°48′	74°52′	9/81	4
118	35°46′	74°51′	3/77	3
118	36°27′	74°47′	9/77	2
120	36°20′	74°48′	3/77	7
120	36°20′	74°48′	3/78	1
120	37°42′	74°15′	9/79	1
120	36°10′	74°48′	9/80	2
125	36°20′	74°55′	3/79	4
133	34°56′	75°21′	3/79	2
135	35°00′	75°16′	9/79	4
137	35°33′	74°49′	3/76	21
170	36°10′	74°47′	3/76	1
173	35°51′	74°52′	3/82	4
183	35°41′	74°49′	9/77	8
186	34°21′	75°55′	3/82	1
188	34°52′	74°24′	3/79	1
189	35°40′	74°48′	3/79	7
[1]189	35°39′	74°48′	9/81	7
205	35°53′	74°50′	3/76	18
205	35°37′	74°49′	10/76	12
220	35°50′	74°51′	9/79	2
228	34°27′	75°44′	9/79	1
246	36°25′	74°46′	3/76	10
290	35°20′	74°54′	3/80	3

shelf is more limited than its estuarine distribution. Although substantial shelf populations are restricted to the south and west of Long Island, NY, breeding populations are found in estuaries as far north as Hog Bay, ME (44°35′N) (Born 1977). Populations in Narragansett Bay, Barnstable Harbor, Buzzards Bay, Cape Cod Bay, and Nantucket Harbor are large enough to be commercially exploited for *Limulus* lysate and/or bait (Botton and Ropes in press). Why such populations remain close to shore is unclear. However, it is consistent with the data of Baptist et al. (1957). They showed that individuals in Plum Island Sound, MA, remained in the local area 3 years after tagging.

The more northerly horseshoe crabs may be more discrete and isolated estuarine populations than those from North Carolina to New York. The small number of crabs on the southern New England shelf suggests that migrations of crabs between estuaries may be limited, although such populations may be occurring at depths too shallow to be sampled by large vessels. However, in the September 1985 trawl survey of the territorial waters of Massachusetts, only 34 horseshoe crabs were caught at 16 of the 94 stations sampled (mean depth 28 m, range 6-76 m) with similar numbers recorded during other recent surveys (B. Kelly[4]). If, in fact, these New England populations are isolated from the large Virginia-New Jersey stock, overexploitation may have serious detrimental effects. Although horseshoe crab larvae are weak swimmers, they are not commonly found in the plankton. Dispersal between discontinuous New England estuaries therefore depends on migration of juveniles or adults. However, the issue of stock identity may require further study. Shuster (1979) argued, based on morphometric data, that horseshoe crabs formed discrete populations throughout the geographic range. On the other hand, Saunders et al. (1986) found no evidence for genetic divergence between New England and middle Atlantic populations, based on their analysis of mitochondrial DNA.

The most noteworthy feature of the bathymetric distribution was the presence of horseshoe crabs at the edge of the continental shelf, at depths to 290 m. These animals were concentrated off North Carolina, where the continental slope is much closer to shore than at any other location in the Middle Atlantic Bight. This suggests that distance from shore, rather than depth per se, limits the dispersal of crabs on the continental shelf. Horseshoe crabs are eurythermal, tolerating temperatures from −1.1° to over 40°C (Mayer 1914; Fraenkel 1960); neither of these extremes are likely on the northwestern Atlantic continental shelf. Laboratory animals in an electronic shuttlebox arrangement voluntarily occupied temperatures from 15° to 40°C (Reynolds and Casterlin 1979), but the avoidance of cooler water may not apply to all populations, as all experimental animals were indigenous to the Gulf of Mexico. Our depth record at 290 m exceeds the 200 m record of Wolff (1977) but is not the maximum depth attained by this species. A submersible camera operated by the Duke Univeristy Marine Laboratory photographed a horseshoe crab at 1,097 m depth at 32°38′N, 76°33′W (D. Bunting[5]).

The potential orientation cues directing such deep-water animals to and from estuarine spawning beaches are of interest. Rudloe and Herrnkind (1976) showed that wave surge was important in determining the orientation of crabs in shallow waters near breeding sites, while Barlow et al. (1982) found that visual cues are important in the selection of cement "female models" by spawning males. Horseshoe crab eyes are sensitive to polarized light (Waterman 1950) and to low levels of visible light, and there are a variety of endogenous morphological changes that may permit photoreceptors to have high light sensitivity (Barlow et al. 1980). Whether such physiological properties are ecologically significant in enabling crabs to orient from the edge of the continental shelf to the estuarine spawning beaches is not yet known.

Much remains to be learned about the ecological relationships between horseshoe crabs and other shelf fauna. Botton and Haskin (1984) found that adult horseshoe crabs were dietary generalists off the New Jersey coast, both in terms of taxa and sizes of food items selected. Predation by horseshoe crabs in Delaware Bay affects bivalve abundance, size-frequency patterns, and spatial distributions (Botton 1984b, c). Significant commercial fisheries for surf clams, *Spisula solidissima*, and ocean quahaugs, *Arctica islandica*, overlap the range of horseshoe crabs on the northwestern Atlantic continental shelf. A study of horseshoe crab stomach contents is in

[4]B. Kelly, Massachusetts Department of Marine Fisheries, East Sandwich, MA 02537, pers. commun. October 1985.

[5]D. Bunting, Duke University Marine Laboratory, Beaufort, NC 28516, pers. commun. April 1985.

progress which will evaluate the importance of horseshoe crab predation to these bivalves.

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APPENDIX TABLE 1.—Abundance and frequency of occurrence of horseshoe crabs on the middle Atlantic continental shelf. Based on National Marine Fisheries Service trawl surveys from all seasons, 1975 to 1983.

Latitude/ longitude	No. stations sampled	No. stations with crabs	No. crabs	% occurrence	$\bar{x}$/trawl
41°N, 72°W	2	0	0	0.0	0.00
41°N, 71°W	187	0	0	0.0	0.00
41°N, 70°W	181	3	10	1.6	0.06
40°N, 74°W	13	4	9	30.8	0.69
40°N, 73°W	396	122	355	30.8	0.90
40°N, 72°W	399	39	72	9.8	0.18
40°N, 71°W	318	0	0	0.0	0.00
40°N, 70°W	303	0	0	0.0	0.00
39°N, 74°W	269	134	999	49.8	3.71
39°N, 73°W	250	5	9	2.0	0.04
39°N, 72°W	255	0	0	0.0	0.00
39°N, 71°W	61	0	0	0.0	0.00
39°N, 70°W	23	0	0	0.0	0.00
38°N, 75°W	92	74	1,208	80.4	13.13
38°N, 74°W	390	167	1,986	42.8	5.09
38°N, 73°W	233	1	1	0.4	0.04
38°N, 72°W	34	0	0	0.0	0.00
37°N, 75°W	323	174	1,085	53.9	3.36
37°N, 74°W	264	16	21	6.1	0.08
37°N, 73°W	7	0	0	0.0	0.00
36°N, 75°W	297	80	456	26.9	1.54
36°N, 74°W	183	17	54	9.3	0.29
35°N, 76°W	2	1	1	50.0	0.50
35°N, 75°W	247	77	413	31.2	1.67
35°N, 74°W	78	31	234	39.7	3.00
34°N, 77°W	102	4	4	3.9	0.04
34°N, 76°W	218	30	114	13.8	0.52
34°N, 75°W	75	3	3	4.0	0.04
33°N, 77°W	144	1	1	0.7	0.01
33°N, 76°W	58	0	0	0.0	0.00

NOTES

ANALYSIS OF SEA TURTLE CAPTURES AND MORTALITIES DURING COMMERCIAL SHRIMP TRAWLING

Five species of sea turtles occur in coastal United States waters of the southern North Atlantic and the Gulf of Mexico and are listed and protected under the Endangered Species Act (1973). These are the Kemp's ridley turtle, *Lepidochelys kempi*; hawksbill turtle, *Eretmochelys imbricata*; leatherback turtle, *Dermochelys coriacea*; green turtle, *Chelonia mydas*; and loggerhead turtle, *Caretta caretta*. Each of these species are captured by commercial shrimp trawlers, and these incidental captures have been identified as a source of sea turtle mortalities (Hopkins and Richardson 1984).

Several prior studies have attempted to quantify turtle catch rates and mortalities by trawlers through interviews with vessel captains (Anonymous 1976,[1] 1977[2]; Cox and Mauerman 1976; Rabalais and Rabalais 1980) and through direct observations by observers during commercial shrimp trawling (Hillestad et al. 1978; Ulrich 1978[3]; Roithmayr and Henwood 1982[4]). While these studies provide estimates of capture and mortality rates, more specific information is required to effectively protect the stocks. In particular, managers need to know when and where turtle captures occur, which species are impacted, at what depths the majority of captures occur, and how many turtles are captured and killed.

This report provides a preliminary analysis of existing data collected by fisheries observers during commercial U.S. shrimp trawling. Data from three National Marine Fisheries Service (NMFS) observer projects were used for analysis of turtle catch per unit effort (CPUE) and mortality rates. A brief description of the projects follow:

1) The sea turtle incidental catch and mortality project was instituted to provide information on the incidental capture and associated mortality of sea turtles off the southeastern United States. Trained fishery observers were placed aboard commercial shrimp vessels operating on the major grounds in the Gulf of Mexico and southern North Atlantic from 1979 through 1981.
2) The goal of the excluder trawl project was to design an apparatus for use with existing shrimping gear which would effectively prevent the incidental capture of sea turtles. Initial design and testing of prototype models were conducted during 1977, and field trials were continued through 1984. Fishery observers aboard cooperative and chartered shrimp trawlers began data collection in 1978. Data collection procedures were similar to those of the incidental catch project except that data records were maintained for each net. In this manner, the performance of excluder nets could be compared with that of standard trawls.
3) The objectives of the shrimp fleet discards project were to estimate the magnitude and species composition of incidental fish captures by the Gulf shrimp fleet. Data were collected through contractual arrangements with state agencies from 1973 through 1978. These agencies placed observers on commercial vessels to obtain at-sea sampling off their respective coasts. Data records similar to those of the other two projects were completed for each tow.

In estimating turtle CPUE and mortalities by species, we restricted our analyses to loggerhead, Kemp's ridley, and green turtles. Leatherback and hawksbill turtles were also captured in shrimp trawls, but the infrequency of captures made predictions of CPUE for these species imprecise. In predictions of CPUE for all species combined, these capture records were included.

Data Analyses

For estimations of turtle CPUE and mortalities, the three observer projects were merged. For each data set, effort (E) was standardized to re-

[1]Anonymous. 1976. Incidental capture of sea turtles by shrimp fishermen in Florida. Preliminary report of the Florida West Coast Survey, University of Florida Marine Advisory Program, 3 p.

[2]Anonymous. 1977. Alabama shrimp fishermen interviews for 1977-1978. Marine Resources Office, Alabama Cooperative Extension Service, 1 p.

[3]Ulrich, G. F. 1978. Incidental catch of loggerhead turtles by South Carolina commercial fisheries. Report of the National Marine Fisheries Service, Contract No. 03-7-042-35151, 33 p.

[4]Roithmayr, C., and T. Henwood. 1982. Incidental catch and mortality report. Final report to Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, 20 p.

flect hours towed with a single, 30.5 m headrope length net using the formula

$$E = (\text{nets} * \text{length} = 30.5\text{ m}) * (\text{min} = 60)$$

where nets = number of nets towed,
length = headrope length of a net (meters),
min = minutes fished.

Turtle CPUE ($\hat{R}$) and 95% confidence interval (C.I.) were calculated according to methods described in Snedecor and Cochran (1967) using the formulae

$$\hat{R} = \sum_{i=1}^{n} T_i \Big/ \sum_{i=1}^{n} E_i$$

$$95\%\text{ C.I. on } R = \hat{R} + 1.96\,(1/\overline{E})\sqrt{\sum_{i=1}^{n} (T_i - RE_i)^2/n(n-1)}$$

where R = CPUE (turtles/30.5 m net hour),
$\hat{R}$ = estimated CPUE,
T_i = number of individuals (turtles),
E_i = effort (30.5 m net hour),
n = sample size (number of tows).

The data were stratified by species, season, depth, and statistical zone (corresponding to those used by NMFS for reporting shrimp landings). For each zone, turtle CPUE, mean depth of capture, mean length of tow, and mortality were computed. In summarizing the data, the Gulf of Mexico was subdivided into eastern (NMFS statistical zones 1-7, corresponding to the Florida west coast excluding the panhandle), central (NMFS statistical zones 8-17, corresponding to the Florida panhandle through Louisiana), and western (NMFS statistical zones 18-21, corresponding to the Texas coast) areas. The southern North Atlantic area included the east coast of the United States from Florida to North Carolina, statistical zones 24-33. Part of zone 28, the Cape Canaveral ship channel and adjacent shrimping grounds (lat. 28°15′N to 28°30′N) was excluded to avoid positively biasing CPUE estimates. This habitat harbors large concentrations of turtles throughout the year, and high turtle catch rates (0.3643 ± 0.0045 turtles/hour)[5] do not reflect those occurring on the shrimping grounds outside the Canaveral area. Exclusion of these data is not expected to cause an underestimate of mortalities for the southern North Atlantic because commercial shrimping effort near Cape Canaveral is restricted to three or four vessels during most of the year.

Estimates of shrimp fishing effort for the offshore Gulf of Mexico shrimp fishery were obtained from the NMFS Galveston Laboratory (E. Klima[6]). The shrimp fishing effort was corrected for relative amounts of effort by single rigged, double rigged, and quad rigged vessels and then standardized to 30.5 m net hours. The Atlantic shrimp fishing effort was based on an effort estimate developed in 1983 (Anonymous 1983[7]). Because the data were being updated, more current Atlantic shrimp fishing effort data will be available at a later time.

Percent mortality of the total catch was estimated by a least squares linear regression using percent mortality as dependent upon minutes fished which yielded the relationship of $Y = 0.00165X - 0.03$. The average mortality over 30-min increments of tow length was calculated, and 10 unweighted means were regressed on minutes fished. Although this approach may violate the assumption of homogeneity in regression, it was assumed to be the most appropriate means of describing this relationship, since the dependence of mortality on tow time is strongly statistically significant ($r = 0.98$; $P < 0.001$). Percent mortality was multiplied by turtle captures ±95% upper and lower confidence bounds of turtle captures to estimate the number of turtles killed.

Results and Discussion

Turtle captures and mortality by statistical zone and season with associated trawling effort data were analyzed. While the total observer effort in the Gulf of Mexico (16,771 hours) was greater than the southern North Atlantic (9,943 hours), 482 turtles were captured in the southern North Atlantic and only 52 were captured in the

[5]Means ± the 95% confidence interval will be used throughout the paper.

[6]E. Klima, Southeast Fisheries Center Galveston Laboratory, National Marine Fisheries Service, NOAA, 4700 Avenue U, Galveston, TX 77550, pers. commun. Summer 1986.

[7]Anonymous. 1983. Environmental assessment of a program to reduce the incidental take of sea turtles by the commercial shrimp fishery in the southeast United States. U.S. Department of Commerce, National Marine Fisheries Service, 9450 Koger Blvd., St. Petersburg, FL 33702.

Gulf of Mexico (Table 1). This indicates that per unit effort, 16 turtles were captured in the Atlantic for every one turtle captured in the Gulf.

An attempt was made to compare mean depth and duration of tow for turtle captures with the mean depth and duration of tow for all effort by area with and without turtle captures. The mean depth of fishing and mean length of tow were computed from effort data for each statistical zone and for tows in which loggerhead, Kemp's ridley, or green turtles were captured. In most cases (particularly the Gulf of Mexico) sample sizes were small, and no patterns or consistency were evident. We suggest that despite some apparent statistical differences which we attribute to small sample sizes, average depth and tow duration of turtle captures were probably not different from that of the effort.

Summary information on observer effort, CPUE, shrimping effort, estimated captures, and estimated mortality in the Gulf of Mexico and southern North Atlantic are presented for loggerhead, Kemp's ridley, and green turtles (Table 1). Estimated CPUE for all turtles in the Gulf of Mexico (zones 1-21) was 0.0031 ± 0.0008 turtles/net hour, and CPUE for the southern North Atlantic (zones 24-33) was 0.0487 ± 0.0041 turtles/net hour.

The calculation of estimated mortality used minutes fished as a means of estimating the percent of the turtles captured that are killed. Based on mean tow times from our effort data, the overall mortality rate for the Gulf of Mexico is 29%. The eastern Gulf mortality rate is 34%, the central Gulf rate is 22%, and the western Gulf rate is 38%. For the Atlantic coast, the rate is 21% reflecting the shorter average duration of trawl tows on this coast.

The mortality rates based on minutes fished do not distinguish among species. This is because of the small numbers of captures for species other than loggerhead turtles. If there are differences in the ability of the other turtle species to survive long periods of immersion and the stress involved in being captured in a trawl, the differences are not measurable from these data.

In using minutes fished to estimate mortality, the data did not conform to expected models over the range of our observations. In tows of <60-min duration, mortality rates were <1% suggesting that the logistic model might be most appropriate to describe the relationship. However, of logistic, 2d and 3d order polynomial and linear models, the best fit over the range of tow times observed in these studies was provided by the linear model. In tows of <60-min duration and in tows longer than 360 minutes, the linear model is probably inappropriate; mortality is negligible in very

TABLE 1.—Observer effort, turtle captures, CPUE, shrimping effort, estimated captures and estimated mortality of loggerhead, Kemp's ridley, and green turtles in the Gulf of Mexico and the southern North Atlantic.

Area	NMFS observer effort (net hours)	Number of turtles	CPUE + 95% C.I. on CPUE (turtles/net hour)	Annual shrimping effort (net hours)[1]	Estimated captures (turtles/yr)	Estimated mortality (turtles/yr)
Loggerhead turtles, *Caretta caretta*						
Atlantic	9,943	453	0.0456 ± 0.0039	704,376	32,120 ± 2,747	6,745 ± 577
Gulf of Mexico						
eastern	2,589	12	0.0046 ± 0.0026	611,530	2,813 ± 1,590	956 ± 541
central	6,353	14	0.0022 ± 0.0012	2,391,498	5,261 ± 2,870	1,157 ± 631
western	7,829	16	0.0020 ± 0.0010	1,312,670	2,625 ± 1,313	998 ± 499
overall	16,771	42	0.0025 ± 0.0008	4,315,698	10,789 ± 3,453	3,129 ± 1,001
Kemp's ridley turtles, *Lepidochelys kempi*						
Atlantic	9,943	18	0.0018 ± 0.0008	704,376	1,268 ± 564	266 ± 119
Gulf of Mexico						
eastern	2,589	0	0	611,530	[2]245 ± 245	83 ± 83
central	6,353	2	0.0003 ± 0.0004	2,391,498	717 ± 957	158 ± 210
western	7,829	4	0.0005 ± 0.0005	1,312,670	656 ± 656	249 ± 249
overall	16,771	6	0.0004 ± 0.0004	4,315,698	1,726 ± 1,726	501 ± 501
Green turtle, *Chelonia mydas*						
Atlantic	9,943	7	0.0007 ± 0.0003	704,376	493 ± 211	104 ± 44
Gulf of Mexico						
eastern	2,589	0	0	611,530	[2]61 ± 122	21 ± 41
central	6,353	2	0.0003 ± 0.0003	2,391,498	717 ± 717	158 ± 158
western	7,829	0	0	1,312,670	[2]131 ± 262	50 ± 100
overall	16,771	2	0.0001 ± 0.0002	4,315,698	432 ± 863	125 ± 250

[1]Gulf of Mexcio effort estimates provided by NMFS, Galveston Laboratories (E. Klima text footnote 5) and southern North Atlantic effort based on estimates from Anonymous 1983

[2]Based on CPUE for the overall Gulf of Mexico.

short tows and never reaches 100% because turtles may be captured at any time during the tow and will survive if captured in the latter stages. Tows shorter than 1 hour and longer than 6 hours, however, are relatively uncommon in commercial shrimping operations.

In the southern North Atlantic, the CPUE for all turtles was strongly dependent on depth (Fig. 1). In depths >10 fathoms, turtle captures were rare, even though, based on aerial surveys (Fritts et al. 1983), turtles are distributed well offshore in waters considerably deeper than 10 fathoms. The strong depth dependency of CPUE may reflect the fact that the continental shelf is relatively narrow along the southeastern seaboard, and the fact that most shrimping occurs in waters <10 fathoms. In the Gulf of Mexico, CPUE appeared to be relatively constant over all depths (Fig. 1).

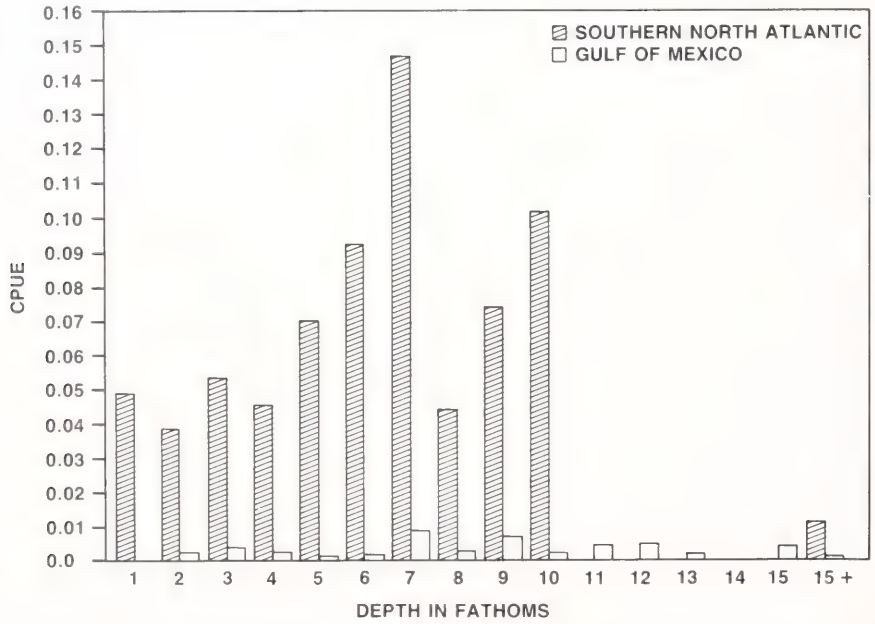

FIGURE 1.—Catch per unit effort (turtles/net hour) as a function of depth for captures in the southern North Atlantic and the Gulf of Mexico.

Conclusions

From our analyses, it is evident that significant numbers of sea turtles are captured by commercial trawlers in both the Gulf of Mexico and the southern North Atlantic, and that over 20% of these turtles are drowned in the trawl. We estimate that 9,874 loggerhead, 767 Kemp's ridley, and 229 green turtles may be killed annually. These estimates are conservative because only offshore (outside the barrier islands) effort and turtle captures were considered.

It should be emphasized that trawl related turtle mortalities are not confined to U.S. waters, but occur on a worldwide basis. The same turtle populations impacted in U.S. waters are also impacted in territorial waters of other countries. In the case of the Kemp's ridley which is believed to be equally distributed in United States and Mexican waters, Mexican trawlers may account for mortalities similar to those of U.S. trawlers. To effectively protect sea turtles, international cooperation is essential.

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THE RELATIONSHIP BETWEEN LUNAR PHASE AND GULF BUTTERFISH, *PEPRILUS BURTI*, CATCH RATE

Through the joint efforts of Japan and the United States, a research program was conducted in fall 1984 and spring 1985 to identify squid resources in the northern Gulf of Mexico (Grace 1984, 1985). Although large concentrations of squid were not located, commercial quantities of gulf butterfish, *Peprilus burti*, were encountered. Maximum sustainable yield (MSY) estimates from the spring data indicated annual potential catches of 50,000 t with a projected ex-vessel value of $19 million (Gledhill[1]). Although gulf butterfish are sufficiently abundant to support a fishery, critical gaps of information on gulf butterfish distribution and location exist which are needed in order to harvest this resource efficiently. Preliminary data from the U.S.-Japan joint surveys indicated that gulf butterfish catch rates were greatest at bottom temperatures of 15°-19°C. Subsequent scientific and commercial efforts at targeting gulf butterfish based upon bottom temperature have produced catches ranging from few individuals to many tons. In a recent study, we found that fishing success for gulf butterfish was often high for several days followed by periods of low success (Allen et al. 1986). This phenomena parallels catch patterns encountered by east coast gulf butterfish fishermen (Amos[2]), who suggest that lunar phase affects catch rates. We analyzed the effect of lunar phase on catch rates. The purpose of this paper is to present evidence that bottom trawling success for gulf butterfish is related to lunar phase.

Methods

Gulf butterfish catches from the two U.S.-Japanese joint surveys and from an additional gulf butterfish survey conducted by SEAMAP (August 1985) were examined. Initially, catch rates per hour of individual trawls were calculated per calendar day. A lunar day value (1-29) was assigned to each calendar day of trawling during the three cruises. Lunar day 1 was assigned to the third calendar day proceeding the new moon on through day 29 falling on the third calendar day following the last quarter moon phase. Mean catch (kg/hour per lunar day) was then calculated and plotted. Catches from trawled stations outside of the depth range in which gulf butterfish were caught during each trip (i.e., $<$ minimum depth or $>$ maximum depth) were not included when calculating mean catch/hour per lunar day.

The effects of moon phase and trip on natural log catch rates ($\ln(x + 1)$, where x = kg/hour per individual trawl) of gulf butterfish were investigated, using the general linear model (GLM) procedures (SAS) Institute (1982). Type III sums of squares were used for the analysis due to unequal number of observations in each subclass. Each observation from each trip was assigned into a lunar phase period (1-4). Mean catch ($\ln(x + 1)$/hour) and number of trawls sampled during each trip and lunar phase are presented in Table 1. An

[1]Gledhill, C. T. 1985. A preliminary estimate of gulf butterfish (*Peprilus burti*) MSY and economic yield. Unpubl. manuscr., 66 p. Southeast Fisheries Center, Mississippi Laboratories, National Marine Fisheries Service, NOAA, Pascagoula, MS 39568-1207.

[2]Duncan Amos, Georgia Marine Extension Program, P.O. Box Z, Brunswick, GA 31523, pers. commun. July 1986.

TABLE 1.—Mean catch (ln(x + 1)/hour) of gulf butterfish and number of trawls sampled during each trip and lunar phase.

Trip	Phase	Number	Mean catch
1	1	6	1.13
1	2	24	2.57
1	3	13	1.58
1	4	31	2.31
2	1	24	2.07
2	2	47	3.24
2	3	9	1.29
2	4	21	2.16
3	1	39	0.49
3	2	35	0.58
3	3	21	0.26
3	4	62	0.40

analysis of variance (ANOVA) model was developed to test for the effect of trip, lunar phase, and the interaction between trip and lunar phase. Scheffe's test was used to contrast each lunar phase with the other three phases.

Results

Peak catch rate was observed to occur in the first quarter moon phase following the new moon (Fig. 1). There was a highly significant difference among trips and lunar phases (Model 1, Table 2). The interaction between trip and lunar phase was not significant ($P = 0.33$) and was therefore dropped from the model resulting in Model 2 (Table 3). In model 2, there was a highly significant difference among trips and a significant difference among lunar phases. A comparison of means using Scheffe's test for each moon phase (Table 4) indicated that catch rate during the first quarter moon phase was significantly greater than catch rates during the last quarter, new, and full moon phases.

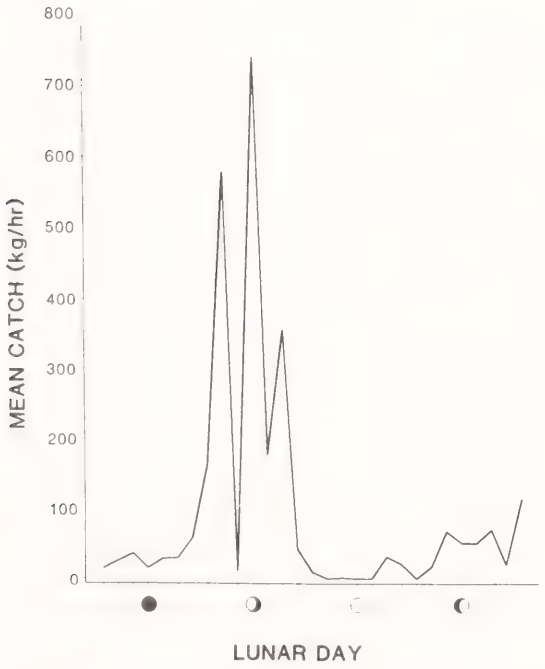

FIGURE 1.—Graph of mean catch (kg/hour) of gulf butterfish by lunar day.

TABLE 2.—Analysis of variance table testing the effects of moon phase (M), research trip (T), and the interaction between trip and moon phase (T * M) on gulf butterfish catch rates during three butterfish research surveys in the Gulf of Mexico 1984-85.

MODEL 1				
Source	df	ss	F-ratio	Pr > F
Model	11	384.864	9.90	0.0001**
Error	320	1,130.662		
TYPE III				
Variable	df	ss	F-ratio	Pr > F
T	2	175.758	24.87	0.0001**
M	3	43.110	4.07	0.0074**
T * M	6	24.353	1.15	0.3338

**Significant effect at $P < 0.01$.

TABLE 3.—Analysis of variance table testing the effects of moon phase (M) and research trip (T) on gulf butterfish catch rates during three butterfish research surveys in the Gulf of Mexico 1984-85.

MODEL 2				
Source	df	ss	F-ratio	Pr > F
Model	5	360.511	20.35	0.0001**
Error	326	1,155.016		
TYPE III				
Variable	df	ss	F-ratio	Pr > F
T	2	272.183	38.41	0.0001**
M	3	37.648	3.54	0.0149*

**Significant effect at $P < 0.01$.
*Significant effect at $P < 0.05$.

TABLE 4.—Mean catch rate per hour (ln(x + 1)/hour) by lunar phase

Lunar phase	Catch rate/hour
New Moon	1.09
First Quarter	2.21*
Full Moon	0.88
Last Quarter	1.24

*$P < 0.05$.

Discussion

Although lunar rhythmicity in marine organisms, particularly marine invertebrates, has long been recognized (Palmer 1974), lunar rhythms in which a single peak of activity occurs each month in fishes appear to be rare (Gibson 1978). Most accounts of variations in catch rate of commercially important species which correlate with moon phase refer to clupeids (Gibson 1978). Blaxter and Holliday (1963) suggested several possible explanations for the apparent lunar rhythmicity of clupeid catches including: 1) intensity of moonlight, 2) effect of tides, and 3) fishermen behavior.

Gulf butterfish are normally trawled during daylight when they concentrate near bottom following nocturnal vertical migration. However, this migration is difficult to describe because conventional echo sounding equipment poorly tracks gulf butterfish movement owing to atrophy of the swim bladder in gulf butterfish over 100 mm standard length (Horn 1970). Differences in catch rates between lunar phases may be attributed to changing vertical movements of gulf butterfish in the water column. The lunar pattern is probably not due to onshore-offshore movement out of the fishery's area of operation. In the three research cruises, sampling was stratified by bottom depth (36-585 m) and data do not suggest horizontal movements of gulf butterfish outside these depths.

In conclusion, further work on lunar rhythmicity relationships of gulf butterfish is needed. Results may greatly enhance commercial and scientific efforts in harvesting and surveying gulf butterfish, respectively, by identifying alternate fishing methods (e.g., midwater trawling) that successfully target gulf butterfish during all moon phases.

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MOVEMENTS OF COHO, *ONCORHYNCHUS KISUTCH*, AND CHINOOK, *O. TSHAWYTSCHA*, SALMON TAGGED AT SEA OFF OREGON, WASHINGTON, AND VANCOUVER ISLAND DURING THE SUMMERS 1982-85

Knowledge of the migration patterns of salmonids in the ocean is an important consideration in developing fishery management plans. Catches of coded-wire tagged salmon in the ocean have yielded much information on general distribution patterns of different stocks and species of salmon (see for example Hunter [1985], Garrison [1985], and Howell et al. [1985]). Other studies have dealt with movements of salmon tagged in offshore waters of the northern North Pacific Ocean (Hartt 1962, 1966; French et al. 1975; Godfrey 1965; Godfrey et al. 1975) and in coastal waters of British Columbia, Washinton, Oregon, and California (Milne 1957; Vernon et al. 1964; Kauffman 1951; Van Hyning 1951; Fry and Hughes 1951). Movements of juvenile salmon in coastal waters of the Gulf of Alaska were studied by Hartt and Dell (1986); in Georgia Strait, British Columbia, by Healey (1980); and in coastal waters off Oregon and Washington by Pearcy and Fisher (unpubl. manuscr.)[1].

[1]W. C. Pearcy and J. P. Fisher. Migration of coho salmon (*Oncorhynchus kisutch*) during their first summer in the oceans. Unpubl. manuscr. College of Oceanography Oregon State University, Corvallis, OR 97331.

Movements of individual maturing salmon off Oregon and Washington are still poorly known. In this paper we examine migration after tagging of salmonids collected during purse seine cruises off the Oregon and Washington coasts from 1982 to 1985 and off the west coast of Vancouver Island, B.C., in 1984.

Methods

Maturing and juvenile salmon were collected by purse seine during May 1982, 1983, and 1985; June 1982-85; July 1984; and September 1982-84. Coho salmon, *Oncorhynchus kisutch*, were classified as maturing or juvenile, based on the length-frequency distribution of the catch in each month. The distribution was usually bimodal and the division between juvenile and maturing coho salmon was about 300 mm FL in May and June, 360 mm FL in July, and 420 mm FL in August and September. Chinook salmon, *O. tshawytscha*, ≤400 mm in all months were arbitrarily classified as juveniles.

Numbered orange Floy[2] tags were applied with a Dennison Mark II tagging gun between the pterygiophores just below the dorsal fin of fish anesthetized with MS-222. Fish were allowed to recover for a few minutes in tanks with circulating saltwater and then were released into the ocean. Date and location of release was recorded for each tagged fish. Condition of the fish after handling varied, but most swam vigorously in the recovery tank and rapidly swam away when released. However, some scale loss almost always occurred and for some individuals was extensive.

Information on movements of coho and chinook salmon was obtained from subsequent recoveries in ocean and terminal fisheries and on spawning grounds or at hatcheries. No reward was offered

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Summary of mark and recovery data for coho and chinook salmon tagged in the ocean off Oregon, Washington, and the west coast of Vancouver Island.

	Maturing coho		Juvenile coho		Maturing chinook		Juvenile chinook	
Year	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)
1982	194	21 (10.8)	0	—	73	3 (4.1)	0	—
1983	142	17 (12.0)	0	—	5	1 (20.0)	0	—
1984	162	10 (6.2)	86	3 (3.5)	56	4 (7.1)	27	0 (0)
1985	215	13 (6.0)	18	0 (0)	37	8 (21.6)	46	1 (2.1)
All years	713	61 (8.6)	104	3 (2.9)	171	16 (9.4)	73	1 (1.4)

	Maturing coho		Maturing chinook	
Other studies:	No. tagged	No. rec. (%)	No. tagged	No. rec. (%)
Fry and Hughes (1951) Tagging off California in 1939-42, 1948, 1949	954	26 (2.7)	6,144	483 (7.9)
Boydston (unpubl.) Tagging off California in 1971 and 1972	3,341	409 (12.2)		
Van Hyning (1951) Tagging off Oregon in 1948 and 1949	506	29 (5.7)	221	11 (5.0)
Kauffman (1951) Tagging off Washington and W. coast Vancouver Is. in 1948 and 1949	65	16 (24.6)	635	33 (5.2)
Milne (1957)	5,458	476 (8.7)	7,194	970 (13.5)

for return of tags. The straight line distance between release and recovery locations indicated the minimum distance travelled (called "net movement") for fish recovered in the ocean. A series of connected straight line tracks were used to estimate net movement of fish recovered in locations where a single line could not be used (e.g., recoveries in Puget Sound). Straight line distance travelled in the ocean was added to distance travelled upstream to estimate net movement for fish recovered in river systems. Approximate latitudinal change was used to estimate net movement of fish for which an accurate recovery location was not known (e.g., "recovered off Coos Bay"). Net migration rate was estimated by dividing net movement by days between release and recovery.

Results and Discussion

Numbers of fish tagged and percentages recovered are summarized in Table 1 for coho and chinook salmon released in different years. Recovery rates were similar for maturing coho (mean 8.6%, range 6-12%) and chinook (mean 9.4%, range 4-22%) salmon. These are similar rates to those found for these two species in other studies (Table 1).

Numbers of fish recovered in different areas from releases off Oregon, Washington, and Vancouver Island are given in Table 2. Simplified migration patterns are shown in Fig. 1. Recoveries of coho salmon released off Oregon were mainly (81%) from the Columbia River and Oregon. Only 11% were recovered in the Strait of Juan de Fuca or Puget Sound. This distribution differs from Van Hyning's (1951) finding that 47% of coho salmon tagged between June and August from Cape Lookout, OR, to the Columbia River were recovered in Puget Sound. Recoveries of coho salmon released off Washington were more widely distributed and 46% were recovered from the Columbia River to Cape Flattery, 20% in Oregon, 23% in the Strait of Juan de Fuca or Puget Sound areas, and 11% in British Columbia.

Estimated net migration of coho salmon between release and recovery (including upstream migration for those recovered in freshwater) averaged 181 km and ranged from 7 to 657 km (Fig. 2A.) Most coho salmon were recovered within 150 days of release. The two fish recoverd after 330 and 380 days were released as juveniles and recovered the following year as adults.

Net migration rates of the maturing coho salmon tagged in coastal waters were generally very low and ranged from 0.1 to 20.4 km/day with a mean rate of 3.6 km/day (Fig. 2B). Coho salmon recovered in the open ocean off Oregon, Washington, or Vancouver Island (circles) had only slightly higher mean rates of movement than those recovered in the Strait of Juan de Fuca or Puget Sound areas (triangles) or those recovered

TABLE 2.—Recovery areas of tagged coho and chinook salmon released off Oregon, Washington, and the west coast of Vancouver Island.

	Recovery areas										
Release areas	Ocean off N. California	Ocean off Oregon	Coastal Oregon bays & rivers	Columbia River	Ocean off Washington	Coastal Washington bays & rivers	Ocean off W. Vancouver Island	Strait of Juan de Fuca	Puget Sound	British Columbia Rivers	Other British Columbia
Coho											
Off Oregon		11	7	3		2		2	1		
Off Washington		6	1	7	8	1	2	3	5	1	1
Off west Vancouver Island							1				
Chinook											
Off Oregon	1	2	2	1	1						
Off Washington		3		3	2					1	
Off west Vancouver Island								2			

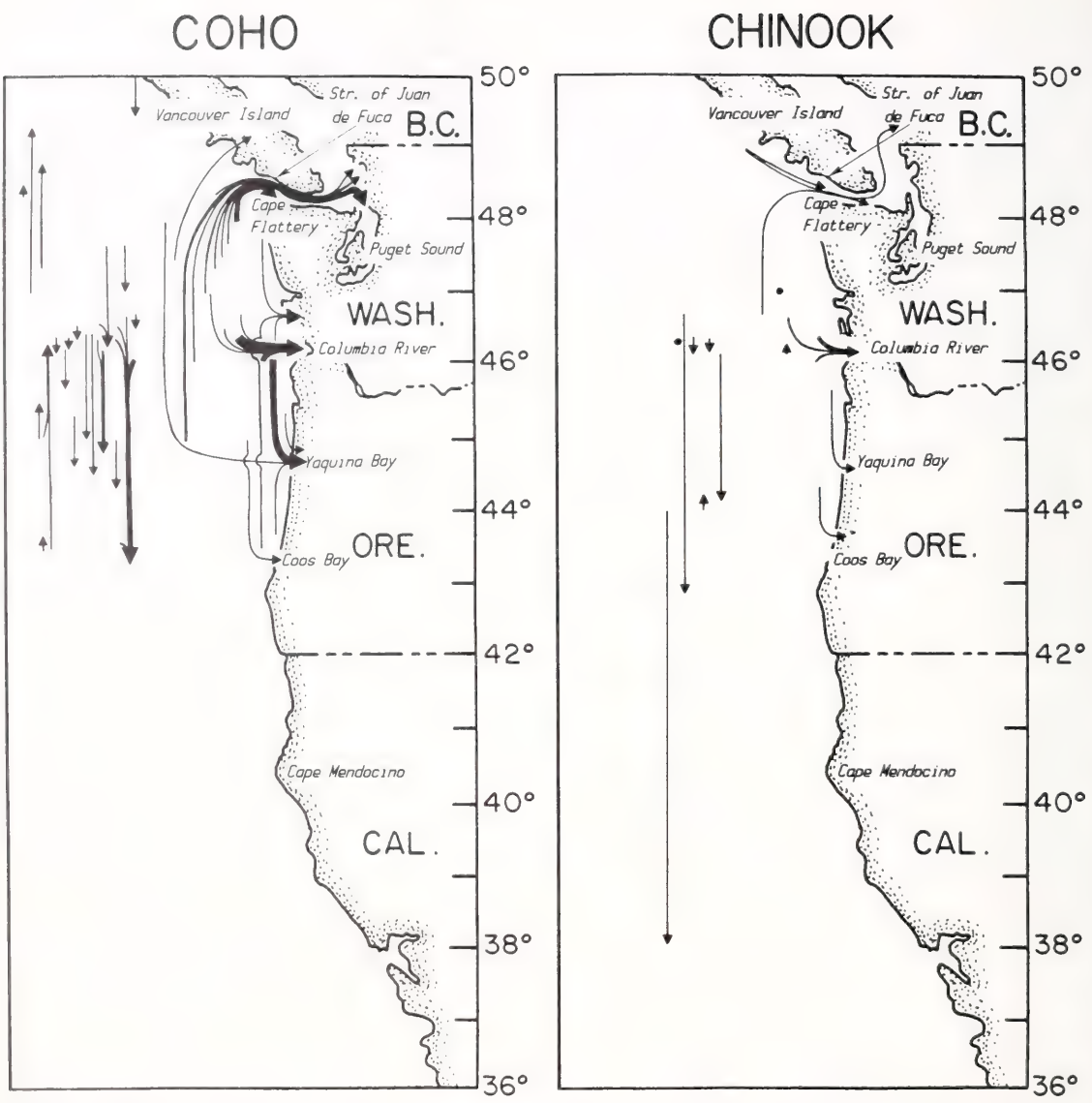

FIGURE 1.—Migration patterns of tagged coho and chinook salmon released at sea. For fish recovered in the ocean off Oregon, Washington, or Vancouver Island, release latitude is indicated by the tail of the arrow and recovery latitude by the head of the arrow. For fish recovered in inland waters or river systems the head of the arrow points to the system in which the fish was recovered. Solid dots indicate fish released and recovered at the same latitude. Numbers of fish are approximately proportional to thickness of arrows. Most releases and recoveries were within 50 km of the coast and the positions of arrows do not represent true distances from shore.

in coastal bays or river systems, including the Columbia River (squares) (4.4, 3.5, and 2.7 km/day, respectively, Fig. 2B). Similar low net movement rates were found for coho salmon in coastal waters by Van Hyning (1951) off Oregon (3.0 km/day), by Kauffman (1951) off Washington and Vancouver Island (3.9 km/day), and by Milne (1957) also off Vancouver Island (9 km/day).

In all studies the stresses related to capture and tagging may cause some mortality and weaken some surviving fish, affecting speed of migration. Hartt (1966) suggested that tagging retards migration by at least 1 day. However, movements of fish immediately after release in sonic tagging experiments were often rapid (Madison et al. 1972; Stasko et al. 1973).

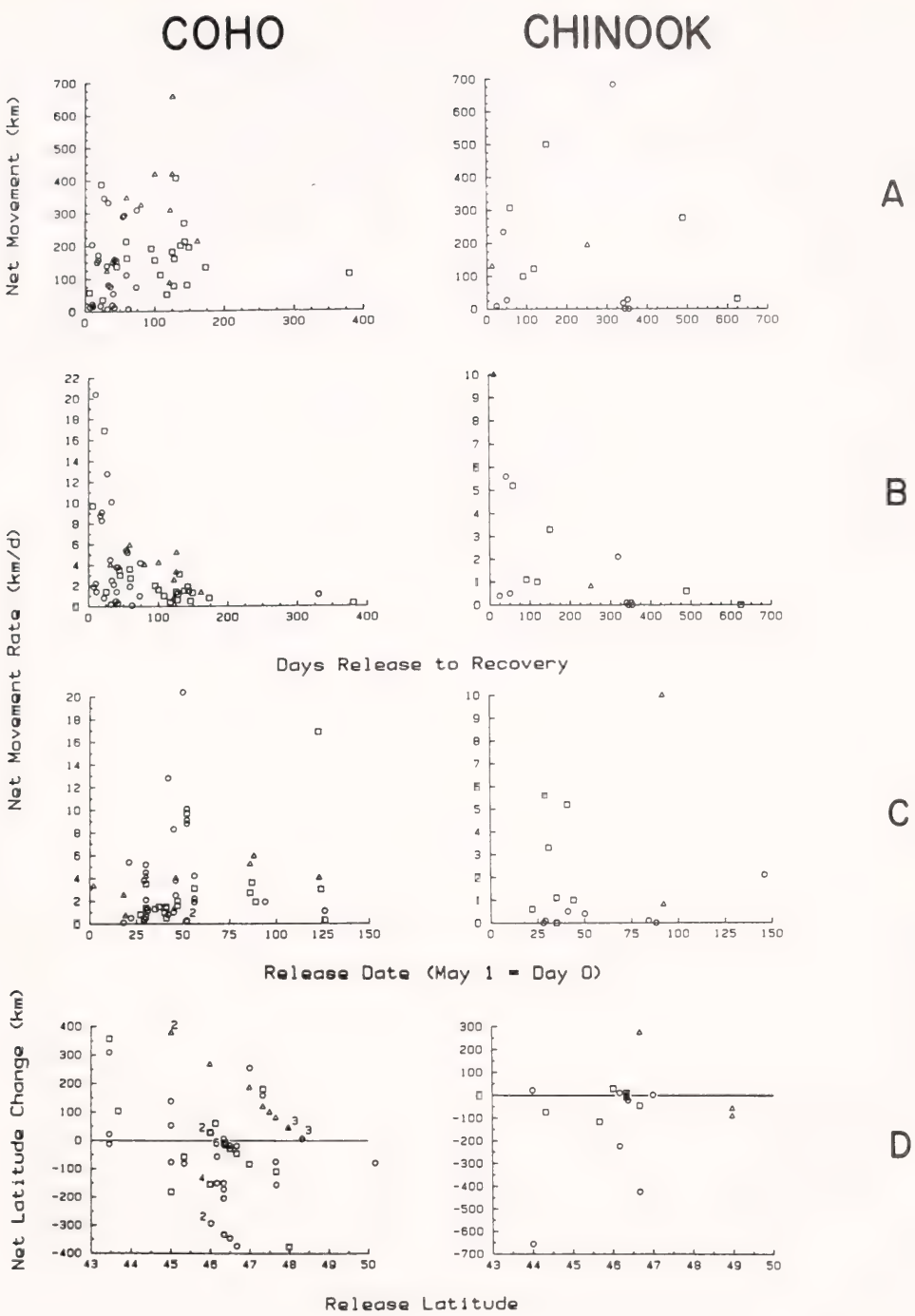

FIGURE 2.—A) net movement vs. days between release and recovery, B) net movement rate vs. days between release and recovery, C) net movement rate vs. release date, and D) net latitude change (+ = north and − = south) vs. release latitude for tagged coho and chinook salmon. Recoveries in inland waters (Strait of Juan de Fuca, Puget Sound, Georgia Strait, and associated river systems) are indicated by triangles, those in the open ocean from the west coast of Vancouver Island to northern California by circles, and those in coastal bays or river systems by squares. For fish released off Oregon or Washington and later recovered in Puget Sound, net latitudinal change (D) is given as the change between the release location and Cape Flattery.

In contrast to the low movement rates observed for coho salmon in coastal waters off Oregon, Washington, and Vancouver Island, net migration rates reported for salmon tagged in offshore waters of the North Pacific were generally much higher. Godfrey et al. (1975) calculated an average rate of 24 km/day for tagged coho salmon recovered in the Japanese high seas fishery and 30 km/day for coho recovered in coastal waters. Hartt (1962, 1966) estimated that the migration rates of sockeye salmon into Bristol Bay averaged 44-50 km/day, whereas those of maturing sockeye salmon caught on the high seas averaged about 32 km/day. Chum salmon had migration rates at sea of 23-50 km/day; pink salmon had average rates of 43 km/day for coastal returns and 50 km/day for high seas returns.

Rapid migrations in coastal waters of British Columbia and Washington were also found for pink salmon (Vernon et al. 1964; Stasko et al. 1973) and for sockeye salmon (Madison et al. 1972) and off the Kurile Islands for chum salmon (Ichihara et al. 1975). However, migration rates slowed greatly as fish neared their home river systems (Vernon et al. 1964; Groot et al. 1975).

Because net migration rates of coho salmon in coastal waters off Oregon, Washington, and Vancouver Island are so much lower than movement rates found for other salmon stocks, these coho are probably spending less time migrating in a single direction compared to meandering and feeding. Similarly, Milne (1957) concluded that coho salmon in coastal waters of British Columbia probably meander during both feeding and spawning migrations. Slow, feeding movements off Oregon and Washington are also suggested by the long time period (3-4 months) during which individual stocks are available in the ocean fisheries (Hunter 1985). The relatively fast net migration rates observed for some coho salmon recaptured within 33 days of release (Fig. 2B) suggest that actual movement rates over short time periods may be quite high but that meandering courses over time produce low net migration rates. Higher migration rates for fish tagged in late summer, to be expected if movements were changing from predominantly feeding to homing, were not apparent (Fig. 2C).

Roughly equal numbers of coho salmon were recovered to the north (27) and to the south (35) of release sites, although most (8 of 11) coho released from lat. 45°N and south were recovered to the north (Fig. 2D). Van Hyning (1951) also found that most coho tagged south of 45°N travelled to the north after release; however, he found that most coho released off northern Oregon and the Columbia River (46°15′N) were recovered to the north as well. Fry et al. (1951) and L.B. Boydston (California Department of Fish and Game, unpubl. data) reported that most recoveries of maturing coho salmon tagged off northern California were to the north, off Oregon or Washington.

Northward migration by most of the maturing coho salmon tagged at sea south of 45°N during their final summer in the ocean is consistent with the distributional patterns of coastal Oregon and early run Columbia River stocks in the ocean fisheries. Peak catches of coastal Oregon coho salmon stocks are off northern California in May and June and shift to waters off Coos Bay in July and August (compiled from Hunter 1985). Relatively high percentages (24-37%) of the ocean catch of coastal Oregon coho salmon stocks (all combined) are off northern California (Garrison 1985; Hunter 1985; Oregon Department of Fish and Wildlife 1982). Similarly, between 62 and 65% of early run Columbia River stocks are caught south of the Columbia River (Hunter 1985; Howell et al. 1985; Oregon Department of Fish and Wildlife 1982). Therefore, many fish from these two stock groups, which make up a substantial fraction of the coho catch off California and Oregon, migrate south and then migrate north sometime later during the summer to return to their natal systems. Southward migration into waters off northern California and southern Oregon may be advantageous to these coho salmon stocks because of the potentially high food production fueled by strong coastal upwelling during the summer in this area.

Other stocks of coho salmon are caught to the north of where they entered the ocean during their final summer in the ocean. About 47% of the late run Columbia River coho are caught north of the Columbia River in Washington and British Columbia (Howell et al. 1985). Smaller, but significant percentages of other stock groups from the south (early Columbia River, private hatchery, and other coastal Oregon groups) are also caught as maturing adults north of their natal streams. Thus, these fish would eventually have to migrate to the south to return to their natal streams. Therefore, the subsequent southward movement of many of the maturing coho salmon we tagged north of 45°N (Fig. 2D) is not surprising.

The slow net migration rates, prolonged residence in coastal waters, and mixed north and

south net movements suggest that maturing coho salmon in coastal waters of Oregon and Washington, unlike stocks of salmon from the Gulf of Alaska and Bering Sea regions, are not highly migratory with precisely directed and timed movements. Many juvenile coho salmon off Oregon and Washington also reside in coastal waters and do not appear to undertake rapid or long migrations out of this region (Pearcy and Fisher fn. 1).

Of the 7 recoveries of chinook salmon released off Oregon, 5 were off Oregon, in the Columbia River, or in coastal Oregon rivers; 1 was off northern California; and 1 was off Washington. Of the 9 recoveries of chinook salmon released off Washington, 3 were in the Columbia River, 3 off Oregon, 2 off Washington, and 1 in British Columbia. Two chinook salmon tagged off the west coast of Vancouver Island were recovered in the Strait of Juan de Fuca (Fig. 1, Table 2).

Estimated net migration of chinook salmon averaged 201 km and ranged from 0 to 685 km (Fig. 2A). Unlike coho salmon, which spend only 1 year in the ocean and which were mostly recovered within 150 days of release, almost half of the chinook salmon, which may spend several years in the ocean, were recovered after more than 200 days at liberty. Mean net migration rate of chinook salmon was 1.9 km/day (n = 16, Fig. 2B). As was found for coho salmon, net migration rates of chinook salmon were many times lower than rates found for salmon tagged in offshore waters of the North Pacific Ocean. Therefore, some chinook salmon also appear to undertake meandering feeding movements in coastal waters off Oregon, Washington, and Vancouver Island. There was no evidence for acceleration of migration rate late in summer (Fig. 1C).

Tagged maturing chinook salmon differed from coho salmon in that most moved to the south after release (Fig. 2D). Columbia River and many coastal Oregon stocks of chinook salmon are caught in the ocean fisheries predominantly to the north of Oregon, i.e., north of their natal systems (Wahle et al. 1981; Garrison 1985). Some of the maturing chinook salmon that we tagged may have been moving slowly toward their natal systems from the north. One chinook salmon was recovered 319 days after release over 656 km to the south, off northern California (Figs. 1, 2D).

Other species of salmonids tagged off Oregon and Washington were recovered only in very low numbers. There were only 2 recoveries from 164 tagged pink and 36 tagged chum salmon. The greatest net movement was by a chum salmon tagged on 1 June 1985 off Seaside, OR, just south of the Columbia River and recovered on 8 August 1985 in Hecate Strait, B.C. (great circle distance 830 km). This fish was at liberty for 68 days and its minimum movement rate as 12.2 km/day.

Acknowledgments

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DAILY GROWTH INCREMENTS IN OTOLITHS OF JUVENILE BLACK ROCKFISH, *SEBASTES MELANOPS*: AN EVALUATION OF AUTORADIOGRAPHY AS A NEW METHOD OF VALIDATION

Investigations into the temporal periodicity of growth increment formation in otoliths of larval and juvenile fishes have produced conflicting accounts. Taubert and Coble (1977), Barkman (1978), Wild and Foreman (1980), and Campana and Neilson (1982), among others, have confirmed daily increment formation in otoliths from various species of larval and juvenile fishes. There have been a few studies, however, in which increment counts were not representative of actual age of the fish (Wild and Foreman 1980; Geffen 1982; Neilson and Geen 1982). Nondaily increment formation has been explained by the inclusion of subdaily rings in age estimates as well as by methodological errors in preparing and viewing the otoliths (Campana 1983a; Campana and Neilson 1985). Since size and age of fish, food limitations, and environmental conditions have been suggested to affect increment formation, validation is necessary in each study where fish age is estimated.

Several techniques have been used to validate daily growth increments in larval and juvenile fish otoliths. Fish of known age, raised from fertilization or birth under controlled laboratory conditions, provide the best material to determine frequency of increment formation (Taubert and Coble 1977; Barkman 1978; Tanaka et al. 1981; Miller and Storck 1982). For many species, however, rearing the larvae from birth through the juvenile stage is difficult or impossible. An alternate method of age validation introduces a chemical mark onto those calcified structures which exhibit periodic growth zones, such as otoliths, scales, and spines. The antibiotic oxytetracycline hydrochloride (OTC) has been used most successfully in this manner (Wild and Foreman 1980; Campana and Neilson 1982; Ralston and Miyamoto 1983; Dabrowski and Tsukamoto 1986). The OTC is taken up at the site of calcification and fluoresces bright yellow under ultraviolet light, compared with the blue autofluorescence of normal tissue. Most recently, stable strontium has been used to demonstrate daily increment formation in squid statoliths (Hurley et al. 1985) and in mass marking of coho salmon (Yamada et al. 1979). For some species, a timemark may also be induced on the otolith by stress,

such as cold shock (Mugiya and Muramatsu 1982), or by simply bringing field-captured fish into the laboratory (Boehlert and Yoklavich 1985). Comparing increment counts with number of days following the time-mark accurately estimates frequency of occurrence of the growth increments. Our study evaluates the commonly used OTC and an alternate chemical, the radioisotope calcium-45, in terms of their success as time-markers to validate daily growth increment formation in the otoliths of juvenile black rockfish, *Sebastes melanops*.

Materials and Methods

Young-of-the-year black rockfish, *Sebastes melanops*, ranging from about 2 to 5 g wet body weight and 47 to 64 mm standard length (SL), were collected from a rocky, intertidal area 8 km south of Newport, OR, in July 1982 and from Yaquina Bay, OR, in July 1983. Fish were held in 200 L tanks under ambient water temperature conditions which fluctuated between 13° and 17°C; a ration of ground squid and shrimp was offered ad libitum and photoperiod was maintained at 13 h light and 11 h darkness. After at least 10 days of acclimation to laboratory conditions, fish were anesthetized with MS-222 and injected intramuscularly (midbody below dorsal fin) with a solution of either OTC or calcium-45. Fish continued to feed immediately following injection and handling.

Calcium-45

Fish were injected with a solution of low-calcium physiological saline and calcium-45 ($^{45}CaCl_2$ dissolved in HCl; New England Nuclear).[1] Through preliminary experiments, a dose of 0.1 μCi ^{45}Ca/g wet body weight proved to be optimum for isotope uptake and retention. Four fish each were sacrificed at 1, 4, 12, 24, 48, 72, 96, 120, 144, 168 hours and at subsequent 4-d intervals for 63 days following injection. Three fish were sacrificed after having maintained good health and growth for 1 year following injection. Four nonradioactive fish were sacrificed on the first day of the experiment and used as blanks or controls in determining activity levels of the injected fish.

At the time intervals specified above, fish were anesthetized, blotted dry, measured (nearest mm, SL), and weighed (nearest 0.01 g). Both sagittal otoliths were removed from each fish, rinsed thoroughly in water to remove surface contamination of calcium-45, and stored dry for liquid scintillation counting (LSC) or autoradiography. One otolith from each fish, with the exception of the three 1-yr-olds, was weighed, dissolved in 0.1 mL concentrated HCl, diluted with 10 mL of Beckman Ready-solv EP liquid scintillation cocktail, and assayed for calcium-45 activity in a Beckman LS 8000 liquid scintillation counter. Activity was corrected for decay and quench and expressed as disintegrations per minute (DPM) per mg of sample. The perceived decrease in radioactivity due to the increase in weight of otolith over the experimental period was corrected using the following equation:

$$\text{Corrected activity} = \frac{\text{DPM}}{\text{mg tissue}_{t_f}} \times \frac{\text{weight tissue}_{t_f}}{\text{mean weight tissue}_{t_i}}$$

where t_f is time at sacrifice and t_i is time of experiment initiation. Mean weight of otolith at t_i was obtained from the 4 fish sacrificed prior to injection; since all fish were of similar length at the onset of experimentation, these 4 fish adequately represented size of injected fish.

Four otoliths from time interval 1 hour and two otoliths from each of intervals 4 and 12 hours and 1, 4, 11, 19, 39, 55, and 63 days were prepared for autoradiography. The right otolith of each pair was affixed to a microscope slide with histological mounting medium. The proximal surface of the otolith was ground with 600 grit carborundum paper on a rotating wheel until the focus was just visible and most of the curvature of the otolith was removed. The mounting medium was gently heated and the otolith was turned to expose the distal surface. Grinding was continued until most of the mounting medium was removed from the margins of the otolith. The external surface was polished using jeweler's rouge (3 μm) and the whole slide was immersed in an ultrasonic cleaner to remove all loose particles from the otolith surface. The resulting sagittal section was coated with Kodak NTB3 nuclear emulsion and exposed in a light-tight box for 8 days at 4°C. The autoradiographs were developed in Kodak D-19 developer for 2 minutes, fixed for 5 minutes in

[1]References to trade names do not imply endorsement by the National Marine Fisheries Service, NOAA.

Kodak Fixer, rinsed for 20 minutes in distilled water, and viewed under transmitted light with a compound microscope at 400× magnification to determine presence and location of exposed silver grains. Growth increments were enumerated from the time-mark to the otolith margin. In most of the otoliths, a check (or exceptionally dense band) was noted prior to the deposition of the radioactive mark. The location of this check, in terms of numbers of increments from the time-mark, was also determined.

Oxytetracycline

A stock solution was prepared using 25 mg OTC (Sigma Chemicals Co.) in 5 mL of physiological saline. Each fish received a dosage of 0.5 mg OTC or 0.1 mL of stock solution. This approximates the dosage reported by Mugiya and Muramatsu (1982) for goldfish and Weber and Ridgway (1962) for sockeye salmon smolts. Fish were sacrificed 21 days after injection, weighed and measured, and both sagittal otoliths were removed, cleaned, and stored dry in the dark.

A sagittal section of the right otolith was prepared as previously described. Sections were viewed at 160× magnification, using a compound light microscope equipped with ultraviolet illumination. The fluorescent mark was located with an ocular marker. Increments were enumerated from this mark to the outer margins of the otolith using visible light.

Results and Discussion

Calcium-45

One hundred and three black rockfish were injected with the radioisotope, calcium-45; there were no mortalities during the 63-d postinjection sampling period. Over the course of the experiment, average fish length increased from 52.5 mm (SD = 1.29, $N = 4$) on day zero to 70.5 mm (SD = 8.23, $N = 4$) on day 63; average total body weight increased from 2.3 g (SD = 0.13, $N = 4$) to 8.10 g (SD = 2.60, $N = 4$).

LSC demonstrated that calcium-45 was taken up and retained in the sagittal otoliths of all fish. Incorporation of calcium-45 into the otolith occurred as early as 1 hour following injection, which was the initial sampling interval; mean activity at this time was 1,377 (SE = 329) DPM/mg otolith (Fig. 1). Similar activity values and uptake patterns of calcium-45, up to 72 hours

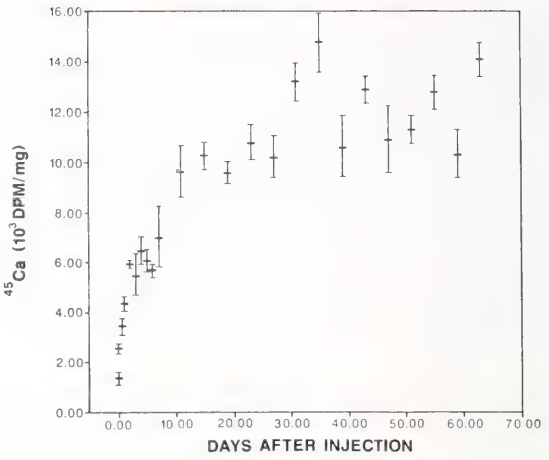

FIGURE 1.—Accumulation and retention of ^{45}Ca in the otolith of black rockfish. Mean activity and 1 SE are indicated. $N = 2$ to 4 fish per time interval.

postinjection, were observed in the otoliths of rainbow trout, although times of maximum incorporation and retention were not assessed over longer periods (Mugiya 1974). Radioactivity in the rockfish otoliths increased sharply for the first 15 days (up to an average of 10,279 DPM/mg, SE = 581), followed by a gradual increase to an apparent asymptote (Fig. 1). The rapid uptake and retention of calcium-45 in liver, muscle, and epidermis of *S. melanops*, and the gradual elimination of the isotope from these tissues (Yoklavich and Boehlert unpubl. data), could contribute to the increase in otolith activity over time; presumably, calcium-45 is transported from these tissues to the otolith via the blood (Mugiya 1974). The lack of decrease in activity in the otolith substantiates the findings of Ichii and Mugiya (1983) and Campana (1983b), which suggest that calcium deposited in otoliths of goldfish and stressed coho salmon, respectively, remains immobilized and is not resorbed. Although no data were presented, it had been suggested earlier by Pannella (1980) that resorption of calcium occurs in the otoliths of some tropical fish species, possibly invalidating ages based on increment counts. Our data show no evidence of resorption, lending support to the usefulness of increment counts in reliably estimating age.

Scattered exposed silver grains were evident along the interface of otolith section and mounting resin in the autoradiographs of otoliths from the earliest sampling periods (1 hour to 1 day), although positive association of the grains with a

distinct site of isotope incorporation into the otolith was not discernible. Since the radioactive mark was on the edge of the otoliths from these early sampling periods, it was more difficult to identify than the mark left on otoliths of fish sacrificed later in the experiment. Distinct bands of silver grains, designating the site of isotope uptake, were evident in all but four otoliths sampled from day 4 through day 63 (Fig. 2). A less dense background of grains spanned 7 to 10 bands around the site of uptake; postinjection increment counts were made from the site of densest grain

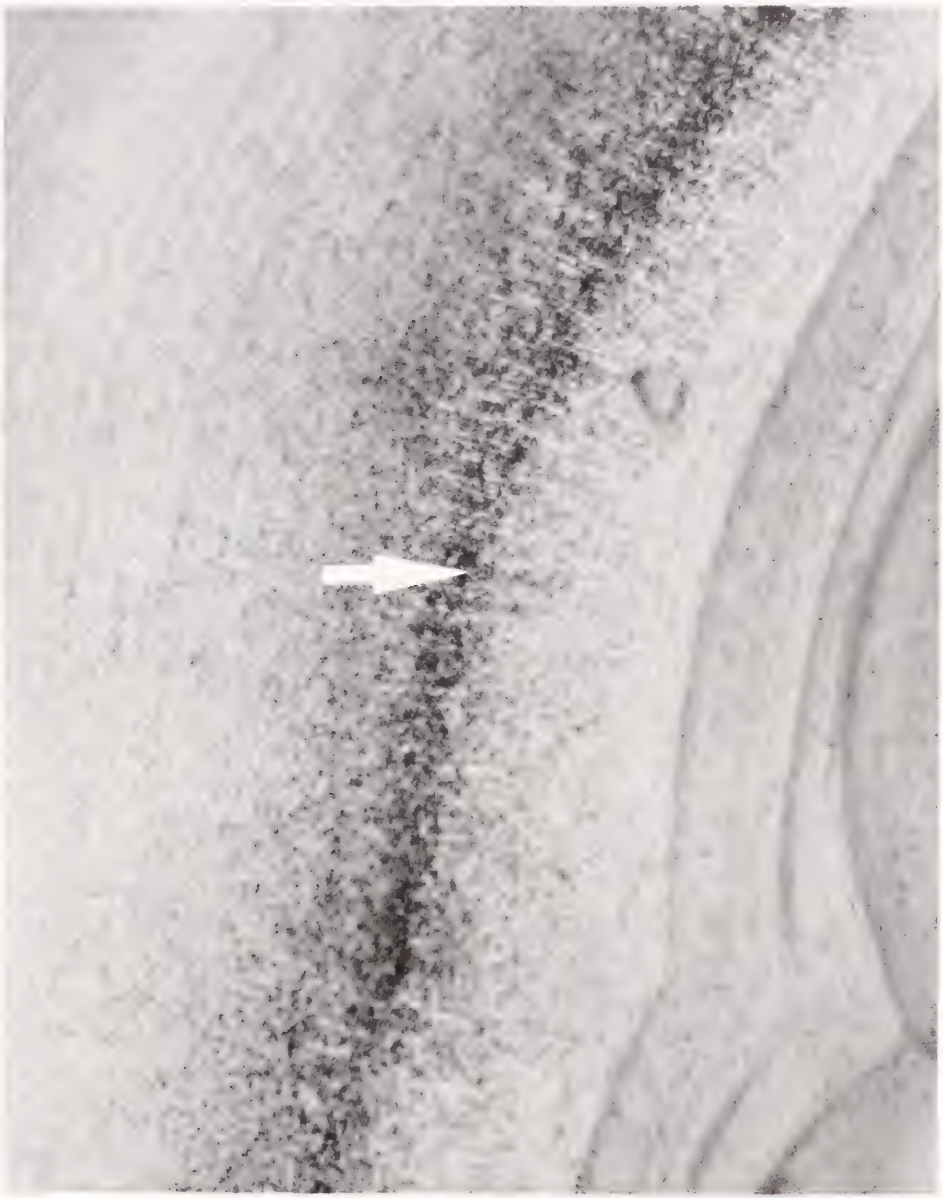

FIGURE 2.—Example of the silver grains produced by the autoradiograph of ^{45}Ca in the otolith of a 69 mm juvenile black rockfish. Arrow indicates band of densest grains; for scale, arrow = 35 μm. This photo is from the anterodorsal region of the otolith. Note the clear increments present on the left side of the figure, representing the increments distal to the time-mark.

accumulation to the edge of the otolith. The posterodorsal area of the sagittal sections showed the heaviest accumulation of the isotope and was also the easiest area in which to count increments. This observation is consistent with Irie (1960) and Mugiya (1974), who concluded that high calcium uptake occurred in the dorsal region, as well as in the anterior and posterior tips of otoliths; these are the regions of fastest otolith growth.

The number of growth increments from the band of densest accumulation of silver grains to the edge of the otolith section closely approximated the number of days the fish were held in the laboratory following injection (Table 1), thereby validating the occurrence of daily growth increments in these juvenile black rockfish. Validation of the frequency of growth increment formation, obtained from fish held under optimal growth conditions in the laboratory, and the apparent lack of otolith resorption, as demonstrated by the increasing retention of calcium-45 with time, suggest that daily increments on otoliths could provide accurate representation of age and growth for field-caught juvenile *Sebastes melanops*. Daily increments have recently been suggested to occur on otoliths of early larvae of *S. marinus* (Penny and Evans 1985). In previous work on juvenile *Sebastes*, growth increments had been counted but not validated (Moser and Ahlstrom 1978; Boehlert 1981). Our study is thus the first confirmation of daily increments on otoliths of juvenile *Sebastes*.

Checks, or exceptionally dense and dark bands deposited as daily increments, were observed in otoliths from fish used in the calcium-45 experiments. One check preceded the radioactive time-mark and another check was associated with the time-mark itself. Ten growth increments were noted from the earliest check to the time-mark in each otolith (Table 1). Formations of checks in otoliths have been documented for many species, including coho salmon (Campana 1983b), goldfish (Mugiya and Muramatsu 1982), and several tropical species (Brothers et al. 1983). Such checks have been attributed to periods of physiological stress to the fish due to collection, migration, change in feeding or habitat, temperature, life history stages, or anything else that disrupts growth. In the present study, the time from fish collection to injection of the isotope marker was 10 days (Table 1). It seems clear that the observed checks were produced as a consequence of stress encountered during capture and transport to laboratory conditions and can be used as additional evidence of daily deposition of growth increments. If such checks are reliably produced, they may be better than chemical time-markers for validation studies such as these.

TABLE 1.—Age validation using otoliths from black rockfish marked with calcium-45 or oxytetracycline. Number of days from capture to injection is compared with number of growth increments from capture check to time-mark; number of days from injection to sacrifice is compared with number of increments from time-mark to margin of otolith.

Treatment/ sample size	Number of days from		Mean number increments from	
	Capture-injection	Injection-sacrifice	Check-mark	Mark-margin
^{45}Ca/4	10	0.04	10	[1]0
/2	10	0.17	10	[1]0
/2	10	0.5	10	[1]0
/2	10	1	10	[1]0
/1	10	4	10	4
/1	10	11	10	11
/1	10	19	10	19
/2	10	39	10	36
/1	10	55	10	55
/2	10	63	10	63
OTC /5		21		21

[1]Scattered silver grains associated with margin.

Oxytetracycline

The OTC was incorporated into the otoliths of each of the 15 fish injected and produced a distinct fluorescent band. The growth increments following injection of OTC, however, were less distinct on most of the otoliths and consequently all otoliths could not be used to validate daily increment formation. Weak increment definition following OTC incorporation in otoliths of larval spot and pinfish has been reported by Hettler (1984). Although Hettler suggested that the lack of distinct increments resulted from experimental stress, postinjection increments were clearly visible in otoliths from the juvenile rockfish which were injected with calcium-45 and held under laboratory conditions similar to the OTC experiments. Five of the rockfish otoliths did display clear growth bands following the fluorescent time-mark; enumeration of these increments is summarized in Table 1. These otoliths show the same results as those from calcium-45 treatments, demonstrating the daily periodicity of growth increment formation in juvenile black rockfish. It is unclear, however, why 67% of the otoliths failed to produce prominent daily increments after OTC incorporation.

The fluorescent OTC mark was more intense

and easier to identify than the exposed silver grains in the autoradiographs of most otoliths. OTC is less hazardous to handle in the laboratory and can be detected in the otolith for much longer periods than calcium-45. The OTC was still visible in the otolith at least 3 years following injection and has in fact been used in studies for mass-marking of fish for identification purposes, where time at liberty may be even longer (Tsukamoto 1985). The activity of calcium-45 was evident in autoradiographs of a few otoliths which were developed 2 years following injection; amount of activity depends upon the effective half-life of the isotope (164 days for calcium-45) and the initial amount of activity in the tissue. An autoradiograph of a transverse section through the otolith of one of the fish injected and held for 1 year revealed a discontinuous band of very faint, exposed silver grains, dispersed primarily over the internal and dorsal areas of the otolith. Association of the isotope with an annular band was not observed. Autoradiographs are difficult to produce, expensive, and time consuming. On the other hand, OTC is simply observed in the otolith section under ultraviolet light. Our recommendations for validating the daily formation of growth increments in juvenile rockfishes are 1) the use of OTC, if growth increments can be routinely identified following injection, or 2) stress marks, which are induced either when transferring fish from the field to laboratory or by subjecting fish to abrupt environmental changes. Where this type of induced stress is not appropriate, as in environmentally controlled laboratory studies, and OTC marking is unsuccessful, marks could reliably be produced with the calcium-45 technique described in this paper.

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47. Reproduction, maturation, and seed production of cultured species. Proceedings of the Twelfth U.S.-Japan Meeting on Aquaculture, Baton Rouge, Louisiana, October 25-29, 1983. By Carl J. Sindermann (editor). February 1987, iii + 73 p. [13 papers.]
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49. Reproduction, movements, and population dynamics of the southern kingfish, *Menticirrhus americanus,* in the northwestern Gulf of Mexico. By Stephen M. Harding and Mark E. Chittenden, Jr. March 1987, iii + 21 p., 8 tables, 10 figs.
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51. Status, biology, and ecology of fur seals. Proceedings of an international symposium and workshop, Cambridge, England, 23-27 April 1984. By John P. Croxall and Roger L. Gentry (editors). June 1987, v + 212 p. [14 Species Summaries; 12 Contributed Papers; 5 Rapporteurs' Report; 1 Bibliography.]
52. Limited access alternatives for the Pacific groundfish fishery. By Daniel D. Huppert (editor). May 1987, iii + 45 p. [8 papers.]
53. Ecology of east Florida sea turtles. Proceedings of the Cape Canaveral, Florida, sea turtle workshop, Miami, Florida, February 26-27, 1985. By Wayne N. Witzell (convener and editor). May 1987, iii + 80 p. [11 papers.]
54. Proximate and fatty acid composition of 40 southeastern U.S. finfish species. By Janet A. Gooch, Malcolm B. Hale, Thomas Brown, Jr., James C. Bonnet, Cheryl G. Brand, and Lloyd W. Regier June 1987, iii + 23 p., 43 tables.

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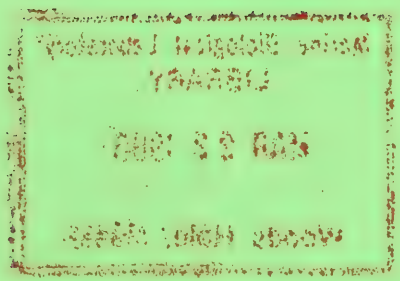

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